The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 7. Cycadophyta

W.B. Keith Holmes[1] and Heidi M. Anderson[2]

[1]46 Kurrajong Street, Dorrigo, NSW, 2453, Australia (Hon. Research Fellow, University of New England, Armidale, NSW, 2351); [2]46 Kurrajong Street, Dorrigo, NSW. 2453, Australia (Hon. Palaeobotanist, South African National Biodiversity Institute, Pretoria 0001 South Africa).

Holmes, W.B.K. and Anderson, H.M. (2008). The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 7. Cycadophyta. *Proceedings of the Linnean Society of New South Wales* **129**, 113-149.

Cycadophyte fronds comprise c. 4% of the catalogued specimens in the Holmes' collections from two quarries in the middle Triassic Nymboida Coal Measures of the Nymboida sub-Basin in north-eastern New South Wales. The fronds are placed in fifteen taxa in the Cycadales and one in the Bennettitales. Eight new species are described; *Pseudoctenis nymboidensis*, *P. rigbyi*, *P. prolongata*, *P. cursanervia*, *P. grandis*, *P. nettiana*, *Moltenia sparsispinosa* and *Ctenis marniana*. *Halleyoctenis megapinnata* is nominated as a new genotype for *Halleyoctenis*.

Manuscript received 24 June 2007, accepted for publication 6 February 2008.

KEYWORDS: Cycadophyta, Middle Triassic flora, Nymboida Coal Measures, palaeobotany.

INTRODUCTION

This is the seventh part of a series describing the early-middle Triassic Nymboida flora Part 1 (Holmes 2000) of this series described the Bryophyta and Sphenophyta, Part 2 (Holmes 2001) the Filicophyta, Part 3 (Holmes 2003) fern-like foliage, Part 4 (Holmes and Anderson 2005a) the genus *Dicroidium* and its fertile organs *Umkomasia* and *Pteruchus*, Part 5 (Holmes and Anderson 2005b) the genera *Lepidopteris*, *Kurtziana*, *Rochipteris* and *Walkomiopteris* and Part 6 (Holmes and Anderson 2007) the Ginkgophyta.

A description of the Coal Mine and Reserve Quarries, the source localities of our described material, together with a summary of the geology of the Basin Creek Formation, the Nymboida Coal Measures and the Nymboida Sub-Basin were provided in Holmes (2000).

In this paper, leaves with cycadophyte affinities are described and illustrated. No fertile material has been found. The cycadophytes include both true cycads in the Order Cycadales, and the bennettitites in the extinct Order Bennettitales (=Cycadioidales). The origins of the cycadophytes date back to the Upper Carboniferous (Taylor and Taylor 1993). Cycad survivors of the End-Permian Extinction diversified and reached their maximum development and world-wide distribution during the Mesozoic Era. Reconstructions of the Mesozoic landscape often portray dinosaurs in close association with cycadophytes (White 1990). Cycadophytes have been in a decline over the last 100 ma. and today true cycads are a relatively small group of plants distributed through tropical and warm temperate regions of the northern and southern hemispheres. Extant cycads comprise c. 190 species in c. 11 genera (Jones 1993) and new species continue to be discovered and described (Singh and Radha P 2006). Two species of cycads, *Lepidozamia peroffskyana* and *Macrozamia johnsonii,* still survive in the Nymboida region of northern NSW (Hill and Osborne 2002).

METHODS

The material described in this paper is based mainly on collections made by the senior author and his family from two Nymboida quarries (Coal Mine Quarry and Reserve Quarry) over a period of forty years and on limited specimens in old collections of the Australian Museum, Sydney, and in the Geology

Department of the University of New England, Armidale, as noted in Retallack (1977) and Retallack et al. (1977).

The exact horizon or source of most specimens is uncertain as the plant fossil material was collected mostly from blocks fallen from the working quarry faces. The Coal Mine Quarry has not been exploited for many years but its weathering high-wall exposure provides an excellent cross-section of beds that demonstrate the palaeo-environmental conditions at the time of sedimentation (Retallack 1977). The Reserve Quarry with excellent exposures was active until recent times. During 2006 the whole quarry was bulldozed for "restoration" purposes into a featureless bowl – a great scientific loss!

In the Holmes collections from Nymboida, leaves attributed to the Cycadophyta comprise c. 4% of the 2600 selectively catalogued specimens of the preserved floodplain flora. However, in life, the Cycadophyta may have been more common in upland areas where their remains would have had very little chance of becoming fossilized.

The Nymboida specimens are preserved in mudstones, siltstones and sandstones as carbonaceous compressions or impressions in which the gross morphology is usually well-preserved. However, spores and cuticles have been destroyed by a tectonic heating event during the Cretaceous Period (Russel 1994). Therefore our identification of taxa is based only on characters of gross morphology.

Cycadophyte leaves have been recorded in the Triassic of Gondwana from South America by Frenguelli (1950), Menendez (1951), Stipanicic and Bonetti (1965), Bonnetti (1968, 1972), Artabe (1985), Herbst and Troncoso (2000), Troncoso and Herbst (2000), Ottone (2006); from India by Lele (1956); from South Africa by Du Toit (1927), Anderson and Anderson (1983, 1989, 2003); from Australia by Johnston (1888), Shirley (1897, 1898), Walkom (1917, 1924, 1925, 1928), Jones and De Jersey (1948), De Jersey (1958), Hill et al. (1965), Flint and Gould (1975), Retallack (1977), Rigby (1977), Webb (1980), Holmes (1982) and from Antarctica, a cycad stem (Smoot et al. 1985), a cycad pollen cone (Klavens et al. 2003) and cycad cataphylls (Hermsen et al. 2006). Where possible, identification and comparisons of the Nymboida material have been made from descriptions and illustrations in the above publications. Due to time and geographical separation our material has not been compared with northern hemisphere taxa, i.e. non-Gondwana species.

Type and illustrated material is housed in the Australian Museum, Sydney. Some additional specimens are in the collections of the Geology Department, University of New England, Armidale and the University of Queensland.

SYSTEMATIC PALAEOBOTANY

CYCADOPHYTA

During the Mesozoic Era the cycadophytes comprised two orders, the Cycadales (cycads) and the Bennettitales (cycadioids). They are distinguished essentially by their reproductive organs and frond cuticle structure (Anderson and Anderson 1989, pp 276-279; Taylor and Taylor 1993). In the absence of cuticles and/or fertile structures, as is the case at Nymboida, the correct assignment of cycadophyte fronds is difficult. In this paper we follow Anderson and Anderson (1989, 2003) who, from their large Molteno collections, albeit with little preserved cuticle, classified all their cycadophyte foliage in the Cycadales except for the genus *Halleyoctenis* that was placed in the Bennettitales. The simple leaves belonging to the form genus *Taeniopteris* have been placed in the Bennettitopsida by Anderson and Anderson (2003). Taeniopterid and other simple leaves from Nymboida will be described in a forthcoming paper of this series.

Anderson and Anderson (1989) and Herbst and Troncoso (2000) noted the polymorphic character of their form species especially when large collections were available. They noted the presence of intergrading forms and Herbst and Troncoso (2000) also questioned the erection of some new form species. We acknowledge this as a constant problem in palaeobotanical taxonomy. Despite the sometimes limited material, we have described and separated our Nymboida cycadophyte fronds into form species based on all available characters of frond and pinna gross morphology and especially on venation architecture and density.

Order Cycadales
Family incertae sedis

Genus *Pseudoctenis* Seward 1911

Type species

Pseudoctenis eathiensis (Richards) Seward 1911.

Pseudoctenis fissa DuToit 1927

Figures 1A, B; 2A; 3A–F

Selected references

1927 DuToit *Pseudoctenis fissa,* p. 386, fig. 22 (3).
1968 Bonetti *Pseudoctenis anomozamoides*, Pl. 2, figs 1, 2.
1968 Bonetti *Pseudoctenis* cf. *falconeriana*, Pl. 2, figs 3, 4; Pl. 3, figs 1, 4.
1989 Anderson and Anderson *Pseudoctenis fissa*, p. 286, t. figs 1–11; Pls 155–157, 162 (1–5), 167 (7–18), 323 (1–2).

Description

A very variable small to medium-sized frond, narrow-elliptic to elongate-spathulate, 150–200 mm long, width at mid-lamina 25–90 mm; rachis to 3 mm wide at base tapering distally. Pinnae attached laterally at high angle in lower half, becoming slightly acute apically, opposite to subopposite, mostly separate to the base, or more widely separated and confluent, or with strongly decurrent acroscopic bases; pinna shape from narrow to broad oblong, adjacent pinnae often of irregular width, basal pinnae short and broad becoming more elongated to 2/3 to apex then reducing in length, apical pinnae sometimes conjoined, apices truncate to broadly obtuse or shallowly cleft. Veins departing from rachis at high angle, sometimes forking close to base or in mid-lamina, running parallel to each other to apex; vein density in mid-lamina 14–18/10 mm.

Material

AMF126860, 133960, 133961, 133962, 133963, 133964, 133965, 133968, Coal Mine Quarry; AMF133966, 133967, Reserve Quarry.

Discussion

The Nymboida fossils placed in *P. fissa* reflect the range in size and form of the material from the Upper Umkomaas and Hlatimbe Valley localities in the Molteno Formation of South Africa (Anderson and Anderson 1989) and from Argentina (Bonetti 1968) as listed in the selected references. However, some Nymboida specimens are larger than the Umkomaas material and exceed in size even those from the Hlatimbe Valley locality (Anderson and Anderson 1989, Pl. 167, figs 12–15).

One slab, AMF133963 (Fig.1B), shows two virtually complete leaves aligned probably from a common point of attachment. There is some woody tissue (? stem) close to the base of the fronds but no clear connection.

***Pseudoctenis nymboidensis* Holmes and Anderson sp. nov.**

Figures 4A; 5A, B; 6A–E; 7A; 8A

Diagnosis

Medium to large variable *Pseudoctenis* frond; pinnae closely spaced, spathulate to broad-elliptic to broad-linear, base straight or slightly contracted, apex broadly rounded, vein density 12–16/10 mm, once-forked proximally or medially.

Description

Frond medium to large, probably ovate to broad-elliptic but as no complete specimens are available the total length and shape is unknown, to >300 mm long and >200 mm wide, the leafbase is not known; at mid-frond the rachis is up to 10 mm wide. Pinnae semi-dorsally attached, closely spaced with confluent bases; ranging in form from spathulate to elongate-elliptic to broad linear, adjacent pinnae often differing in width, from 8–20 mm wide and to 105 mm long; attached at high angle to rachis, 75° – 90° on lower and mid-portions of frond, becoming more acute apically, slightly contracted proximal to base, expanding to mid-pinna then contracting slightly to broad obtuse apex or broad-linear with parallel margins. Veins attached straight to rachis or basiscopically decurrent; some veins forking close to rachis and occasionally medially; vein density across mid lamina 12–16/10 mm.

Holotype

AMF133969, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF133970, 133971, 133972, 133973, 133974, 133975, 133976, 133977, 133978, 133979, Coal Mine Quarry; AMF133980, 133981, Reserve Quarry.

Name derivation

nymboidensis – from the type locality – Nymboida Coal Measures.

Discussion

Although complete fronds are not known, *Pseudoctenis nymboidensis* appears to be one of the larger of the Nymboida cycadophytes. The holotype (Fig. 4A) is of two incomplete fronds lying sub-parallel to each and suggesting autocthonous preservation of fronds abscissed from a nearby parent plant. *Pseudoctenis nymboidensis* is relatively common and the specimens include a continuum of

intergrading pinna forms ranging in outline from spathulate (Fig. 5A) when they are somewhat similar to specimens of the Molteno *P. spathulata* Du Toit (Anderson and Anderson 1989, pls 175–178), to broad linear with unconstricted bases (Fig. 6C). The forms with unconstricted bases and longer pinnae (Fig. 8A))are similar in shape to *P. longipinnata* Anderson and Anderson and the much larger *P. brownii* from the Burgersdorp Formation of South Africa (Anderson and Anderson 1989) but differ by the less dense venation. Large fronds from the Ipswich Coal Measures, similar in size and outline to the largest of *P. nymboidensis* specimens, were compared with *P. brownii* (as *Nilssonia* cf *browni* Du Toit) by Jones and DeJersey (1947). These Ipswich leaves differ from *P. nymboidensis* by the denser venation. *Pseudoctenis megaspatulata* Herbst and Troncoso (2000 p. 286) from Chile is a very much larger spathulate frond also with denser venation. The largest specimens of *P. nymboidensis* approach in size *P. grandis* (described below) but differ by the finer denser venation. *Pseudoctenis multilineata* (Shirley) Herbst and Troncoso 2000 differs by the significantly denser venation (see comments under *Halleyoctenis* below).

***Pseudoctenis rigbyi* Holmes and Anderson sp. nov.**
Figures 9A; 10A

Selected references

1917 *Pseudoctenis eathiensis*, Walkom, p. 19, Pl. 7, figs 1,2.
1965 *Pseudoctenis eathiensis*, Hill et al., Pl. T7, fig 5.
1975 *Pseudoctenis eathiensis*, Flint and Gould, Pl. 2, fig. 9.

Diagnosis

Small to medium-sized *Pseudoctenis* frond; rachis stout; pinnae well-separated, decurrent, elongate elliptic to broad linear, apices acute, adjacent pinnae often of irregular width; venation once-forked proximally then straight and parallel to apex; vein density 16–20/10 mm.

Description

A small to medium-sized *Pseudoctenis* frond, length >300 mm long, to 160 mm wide, ovate to broad-elliptic, rachis stout, to 8 mm wide at base, tapering apically. Pinnae well-separated, semi-dorsally attached at 90° near base, more closely-spaced in mid-frond at c. 75° and more acute apically, slightly contracted proximally but base expanded at point of attachment, decurrent to occasionally confluent, broad-linear to elongate elliptic, in mid-frond c. 60–80 mm long, adjacent pinnae often of irregular width, from 3–8 mm, apices acutely rounded but rarely preserved, length to breadth ratio c. 10 to 1 but variable due to irregular pinna widths. Veins forking once close to base then running straight and parallel to apex; vein density in mid-lamina 16–20/10 mm.

Holotype

AMF133982, Australian Museum, Sydney.

Type Locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF133983, 133984, 133985, 133986, UNEF13451, Coal Mine Quarry.

Name derivation

rigbyi, for Dr J.F. Rigby, a long-time researcher of Australian fossil plants.

Discussion

This is an uncommon cycadophyte at Nymboida. The fronds display a range of variation in pinna size and spacing along the frond rachis. The holotype specimen shows three fronds aligned parallel to each other (Fig. 9A), which suggests they may have abscissed from a nearby parent plant. *Pseudoctenis rigbyi* differs from *P. prolongata* (below) by the shorter pinna length to width ratio and to all other Nymboida cycadophytes by the broad linear to elliptic pinnae with variously contracted bases. *Pseudoctenis rigbyi* is close in vein density and pinna shape to some Molteno specimens of *P. gracipinnata* (Anderson and Anderson 1989, pls 159, 160, 168) but is generally a very much larger frond. *Pseudoctenis longipinnata* and *P. harringtonia* from the Molteno Formation (Anderson and Anderson 1989) are similar in venation density to *P rigbyi. Pseudoctenis longipinnata* differs by the larger frond size and by the longer, closely-spaced confluent pinnae; *P. harringtonia* differs by the basally uncontracted and shorter pinnae. In gross morphology the Nymboida specimens are closely similar to fronds referred to *Pseudoctenis eathiensis* (Richards) Seward by Walkom (1917), Hill et al. (1965) and Flint and Gould (1975). We believe the epithet *eathiensis* is inappropriate as it is based on Jurassic material from Scotland. Specimen UQF158 from the Esk Beds of Queensland and listed by Walkom (1917) under *P. eathiensis* has preserved cuticle and was redescribed by Joshi et al. (2004) as

P. pantii. Under the International Code of Botanical Nomenclature (2001), *P. pantii* is a form taxon based only on leaves with cuticle preserved.

Pseudoctenis sanipassiensis Anderson and Anderson 1989

Figures 11A; 12A–C

Reference

1989 *Pseudoctenis sanipassiensis*, Anderson and Anderson p. 289, figs 1, 2.

Description

At Nymboida, known only from incomplete specimens; original length and width not known. Rachis to 5 mm wide. Pinnae semi-dorsally attached from 60° – 90° to the rachis; linear-lanceolate, variable in width, from 4–12 mm, length >90 mm, apices not known, slightly contracted near the base with attachment decurrent to confluent. Veins decurrent on rachis, forking once close to the base then running straight and parallel to the apex; vein density c. 16/10 mm.

Material

AMF133987, 133988, 133989, 133990, 133991, 133992, 133993, 133994, 133995, Coal Mine Quarry.

Discussion

Although incomplete, the above material, except for the semi-dorsal attachment of the pinnae, agrees well with fronds of *P. sanipassiensis* from the Molteno Formation as described and illustrated by Anderson and Anderson (1989 pls 185, 186). It differs from other *Pseudoctenis* spp. with similar venation density by its longer, narrower pinnae.

Pseudoctenis prolongata Holmes and Anderson sp. nov.

Figures 13A; 14A–C

Diagnosis

Small to medium *Pseudoctenis* frond; pinnae well-spaced, very narrow elongate elliptic, length to width ratio 16–23 to 1; vein density 16–20/10 mm.

Description

A small to medium-sized frond, broad elliptic to > 300 mm long and to 200 mm wide; rachis stout, to 5 mm wide at base, tapering apically. Pinnae with semi-dorsal attachment, well-separated, bases expanded, decurrent to barely confluent, attached at high angle but becoming slightly acute towards frond apex, very narrow elongate-elliptic, to 100 mm long in mid frond, 3–5 mm wide; length to breadth ratio of 16–23 to 1, apex acutely rounded. Veins decurrent or straight from rachis, proximally forking once and then running straight and parallel to the acutely-rounded apex; vein density in mid-pinna 16–20/10 mm.

Holotype

AMF133996, Australian Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF133997, 133998, 133999, Coal Mine Quarry; AMF134000, 134001, Reserve Quarry.

Name derivation

prolongata – Latin, *lengthened,* referring to the extremely elongate-elliptic pinnae.

Discussion

Pseudoctenis prolongata differs from all described Gondwana cycadophytes by the long narrow elliptic pinnae. *Pseudoctenis gracipinnata* Anderson and Anderson (1989 p. 240) is somewhat similar but differs by its smaller overall size and shorter pinna length to breadth ratio.

Pseudoctenis nettiana Holmes and Anderson sp. nov.

Figures 15A–G

Diagnosis

A very small *Pseudoctenis* frond; pinnae well-separated, slightly confluent, linear, width irregular, apices obtuse or rarely lobate to lacerate; vein density 24–30/10 mm.

Description

Frond variable from very small to small, lanceolate to broad elliptic, to 100 mm long, c. 40–50 mm wide; rachis c. 2 mm wide at base, tapering distally. Pinnae semi-dorsally attached at a high angle, becoming more acute apically, near frond base well-separated, in mid-frond and apically more closely spaced, slightly confluent, broad to narrow linear, opposite to alternate, adjacent pinnae often of irregular width, 1.5–2.5 mm wide, 15–25 mm long, apices obtuse but on specimen AMF134003 (Fig. 15A) slightly lobed or lacerate. Venation fine, forking close to the base then running straight and parallel to apex; vein density 24–30/10 mm.

Holotype
AMF134003, Australian Museum, Sydney.

Type locality
Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material
AMF134002, 134004, 134005, 134006, 134007, 134008, 134009, Coal Mine Quarry; AMF134010, 134011, Reserve Quarry.

Name derivation
nettiania, for Netta Holmes-Lee, daughter of the senior author, who, for many years, assisted on family collecting trips.

Discussion
The fronds placed in *P. nettiana* are close to the fragmentary type specimen of *P. harringtonia* Bonetti 1968 (Pl. 3, fig 4) and refigured by Anderson and Anderson (1989, Pl. 323, fig. 3). The parameters of *P. harringtonia* were expanded by Anderson and Anderson (1989) to include leaves from the Molteno Formation of South Africa and by Herbst and Troncoso (2000) for leaves from Chile. *Pseudoctenis harringtonia*, as defined by those authors differs from *P. nettiana* by the larger size, coarser venation and the pinnae tapering to an acute apex. *Pterophyllum parvum* Shirley (1898, Pl. 17, fig. 4), an apical portion of a small frond from Queensland, differs from *P. nettiana* by the irregular length and arrangement of the pinnae and by the coarser venation.

***Pseudoctenis grandis* Holmes and Anderson sp. nov.**
Figures 16A, B

Diagnosis
A large *Pseudoctenis* frond, length not known, >260 mm wide, pinnae long, broad-linear; attached semi-dorsally, slightly contracted basally; vein density 22–24/10 mm.

Description
Known from only four incomplete fragments, frond length not known, width >260 mm. Pinnae closely spaced, broad linear, semi-dorsally attached, to >130 mm long but complete pinnae not preserved, 14–17 mm wide, slightly contracted close to the base, apex not known. Veins sometimes forking once proximally then running straight and parallel distally; vein density 22–24/10 mm.

Holotype
AMF134012, Australian Museum, Sydney.

Type locality
Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material
AMF134013, 134014, 134015, Coal Mine Quarry, Nymboida.

Name derivation
grandis – Latin, *large*, referring to the apparent large frond size.

Discussion
This is amongst the largest of known Gondwana cycadophyte fronds. *Pseudoctenis grandis* differs from the large leaf *P. cursanervia* (below) by the veins being more than twice as fine and dense.

***Pseudoctenis cursanervia* Holmes and Anderson sp. nov.**
Figures 17A, B

Diagnosis
A large *Pseudoctenis* frond with broad-linear pinnae, almost parallel-sided, closely spaced but separate to the base, to >175 mm long; veins very coarse, density 10/10 mm.

Description
Based on the rachis and pinna dimensions of the two incomplete specimens with basal and apical portions missing; the complete fronds were very large; rachis to 10 mm wide. Pinnae broad-linear to >175 mm long and 15–20 mm wide, aligned at 90° to the rachis with semi-dorsal attachment, separate to the base, slightly constricted proximally, basiscopic and acroscopic attachment slightly decurrent, apex obtuse. Veins attached straight to the rachis or around the basiscopic and acroscopic margin following the line of the expanded base; some veins forking once at or near the pinna base then running straight and parallel to the apex; veins coarse, to 0.3 mm in width, some veins with two or three longitudinal striations; vein density 10/10 mm.

Holotype
AMF134016, Australian Museum, Sydney.

Type locality
Coal Mine Quarry, Nymboida. Basin Creek

Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF134017 Coal Mine Quarry, Nymboida.

Name derivation

cursa – Latin, *coarse; – nervia* –Latin, *vein*, referring to the coarse venation.

Discussion

Pseudoctenis cursanervia and *P. grandis* (described above) differ by their large broad-linear pinnae from all described Gondwana cycadophyte fronds. *Pseudoctenis cursanervia* differs from *P. grandis* by the much coarser veins. *Pseudoctenis megaspathulata* Herbst and Troncoso (2000), a very large frond from Chile, differs by the spathulate pinnae. *Pseudoctenis brownii* (DuToit 1927) Anderson and Anderson is a poorly-known large leaf with veins apparently closely spaced and differs from *P. grandis* by the moderately contracted pinna bases.

***Pseudoctenis azcaratei* (Herbst and Troncoso) Holmes and Anderson comb. nov.**

Figures 18A–D; 19A

References

2000 *Pterophyllum azcaratei* Herbst and Troncoso, p. 29, figs 2F, 5A, B.

2000 *Pterophyllum azcaratei* Troncoso and Herbst, p.140.

Description

No complete fronds from Nymboida have been collected; mid-frond fragments are up to 100 mm long and to c. 140 mm wide but complete pinnae are rarely present. Rachis to 4 mm wide. Pinnae broad-linear, semi-dorsally attached at c. 90° but becoming inclined apically; adjoining pinnae often irregular in width, closely spaced, 2–6 mm wide, to c. 70 mm long, margins straight and parallel, lamina is not proximally contracted but at point of attachment is slightly decurrent or sometimes confluent with adjacent pinnae. Veins arise straight from the rachis, some forking close to the base or sometimes more distally, then running straight and parallel to the apex; vein density ranges from 26–28/10 mm.

Material

AMF134018, 134019, 134020, 134021, 134022, Coal Mine Quarry.

Discussion

This Nymboida material is closely similar to fronds described as *Pterophyllum azcaratei* from the La Ternera Formation of Chile (Herbst and Troncoso 2000). It differs from all other Nymboida taxa by the broad linear pinnae with very dense venation. We are hesitant in following the *Pterophyllum* generic assignation by Herbst and Troncoso as *Pterophyllum* is essentially a Northern Hemisphere genus and based on cuticle morphology is bennettitalean. From the studies of Anderson and Anderson on the Cycadophyta of the Molteno Formation, it appears that most Gondwana cycad genera are probably cycadalean. As *Pterophyllum azcaratei* is closely comparable in gross morphology with many other *Pseudoctenis* species we believe it is better placed in the latter genus. Future study of specimens with well-preserved cuticle will determine the correct taxonomic assignment.

***Pseudoctenis* sp. cf *Pseudoctenis strahanii* (Johnston) Anderson and Anderson 1989**

Figure 19B

Description

Frond probably medium-sized; fragment preserved 80 mm long, c. 110 mm wide base and apex missing; rachis 3 mm wide. Pinnae well-separated, dorsally attached at high angle to rachis, 5–7 mm wide, to 56 mm long, basiscopic base decurrent, margins parallel, apices irregularly cleft into 2–3 irregular lobes. Basiscopic veins following decurrent base, acroscopically departing straight from rachis, forking once close to the rachis then running straight and parallel into apical lobes. Vein density in mid-lamina 18/10 mm.

Material

AMF134023, Coal Mine Quarry.

Discussion

The above description is based on a single specimen. It is compared with *Pseudoctenis strahanii*, the only previously described *Pseudoctenis* with deeply cleft and lobed pinna apices. The lectotype from Tasmania and illustrated in Anderson and Anderson (1989, pl. 323, fig. 4) differs from the Nymboida specimen by the pinnae with deeper apical clefts and by the less dense venation (12/10 mm). A single specimen of the assemblage placed in *P. nettiana* (see above) has lobed or lacerated pinna apices but differs from *P.* sp. cf. *P. strahanii* by the much smaller size and more dense venation.

Pseudoctenis* sp. *A

Figures 19C, D

Description

This form is known from two apical fragments. Frond small, probably broad-elliptic, length not known, width to c. 60 mm; rachis slender, 1.5 mm wide. Pinnae well-separated to the rachis, bases slightly expanded, semi-dorsally attached at high angle in mid-frond, becoming more acute apically; narrow-oblong with truncate apices, pinnae to 40 mm long, adjacent pinnae irregular in width, 3–6 mm wide. Basiscopic veins decurrent on rachis, others attached straight, most forking once then running straight and parallel to apex. Venation density 20–26/10 mm.

Material

AMF134024, 134025, Coal Mine Quarry.

Discussion

By the elongate-oblong pinnae *Pseudoctenis* sp. *A* is similar to *P. multilineata* (= *Pterophyllum multilineata* of Shirley 1897, fig. 7a and see below) but differs by the much smaller size and less dense venation.

Pseudoctenis* sp. *B

Figure 24A

Description

A *Pseudoctenis* probably of medium size but known from only a single apical fragment. Pinnae well-spaced, attached semi-dorsally to rachis, decurrent to confluent, at high angle then becoming more acute apically on frond; elongate-elliptic, expanding from a narrow base to mid-pinna then contracting slightly distally, > 60 mm long and to 6 mm wide, apices not known. Veins decurrent on rachis then decurving and running parallel to margin to apex, forking once proximally to medially. Vein density across mid-pinna 12–14/10 mm.

Material

AMF134026, Coal Mine Quarry.

Discussion

This is a rare frond form known only from an apical fragment. *Pseudoctenis* sp *B* differs from all other Nymboida cycadophytes by the pinna shape and the coarse venation pattern. In outline *P. gracipinnata* of Anderson and Anderson (1989 p. 290. figs 2–4) is similar to *P.* sp *B* but differs by its larger size and less dense venation.

Genus *Moltenia* Du Toit 1927

The genus *Moltenia* was erected to include cycadophyte foliage with pinnae exhibiting variously serrate margins and lacerated or lobed pinna apices.

Type species

Moltenia dentata Du Toit 1927

***Moltenia sparsispinosa* Holmes and Anderson sp. nov.**

Figures 20A; 21A–D

Diagnosis

Medium-sized *Moltenia* frond; pinnae elliptic with margins very sparsely spinulate; apices truncate or serrate; vein density c. 12–16 / 10 mm.

Description

Frond medium-sized although complete fronds not preserved; probably broad-elliptic in outline; incomplete specimens >185 mm long and to 120 mm wide. Rachis ribbed, slender, 3 mm wide basally and tapering apically. Pinnae broad-elliptic, to 60 mm long and 8–15 mm wide, attached semi-dorsally to rachis at a high angle but becoming more acute apically; variously contracted proximally, bases confluent, apices rarely preserved, cuneate, sometimes serrate; margins entire or with rare and widely-separated short conical spines. Vein attachment at basiscopic base strongly decurrent, midveins straight and acroscopic veins decurrent upwards; veins forking once in an irregular manner – one pinna may have all veins forking close to the rachis while an opposite pinna has veins forking away from the rachis, all then running sub-parallel to the apex; the outermost vein terminates in a spine when present; vein density in mid-lamina c. 12–16/10 mm.

Holotype

AMF134028, Australiam Museum, Sydney.

Type locality

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF134033 paratype; 134027, 134029, Coal Mine Quarry; 134030, Reserve Quarry.

Name derivation

sparsus – Latin, *few, rare*; *spinosa* – Latin, *spiny*

Discussion

The slab bearing the holotype specimen shows three incomplete sub-parallel fronds. Occasional pinnae bear rare small conical marginal spines and

one pinna (Fig. 21A) shows a lacerate apex. On the basis of similar shape and venation, a fragmentary specimen without observable preserved spines, AMF134030 (Fig. 21B) is included in this taxon. *Moltenia sparsispinosa* is closest to *M. paucidentata* Anderson and Anderson (1989, p. 350) but differs by the relatively fewer spines and by the wider but shorter elliptical pinnae. Herbst and Troncoso (2000, fig. 4E) illustrated a frond from Chile as *Pseudoctenis longipinnata* that showed a few distinct serrations and should perhaps be placed in *Moltenia dentata* Du Toit.

Genus *Ctenis* Lindley and Hutton 1834

Type species

Ctenis falcata Lindley and Hutton 1834.

The genus *Ctenis* includes cycadophyte leaves characterized by the laterally attached entire pinnae with veins more or less parallel, anastomosing and meeting the lamina margin (Anderson and Anderson 1989). It is a rare element in Gondwana Triassic floras. Poorly preserved material has been referred to *Ctenis* from Queensland (Jones and DeJersey 1948) and from Argentina (Menendez 1951). Anderson and Anderson (1989) described two species from the Molteno Formation of South Africa.

Two incomplete fronds and their counterparts, described below as *Ctenis marniana* and *Ctenis* sp. *A,* were collected at the Reserve Quarry from the same horizon of grey siltstone. The pinna shape of each specimen and the anastomosing pattern are somewhat different but due to their close proximity they may possibly be fronds from a single variable species. We place them in the genus *Ctenis* on the basis of their clearly preserved anastomosing venation but with reservations as the pinnae are semi-dorsally attached and the outer veins continue parallel to the lamina margin to terminate at the pinna apex.

Ctenis marniana Holmes and Anderson sp. nov.

Figures 22A–C; 23A

Diagnosis

A small pinnate elliptic frond; pinnae at midfrond broad-elliptic, distally conjoining to form entire apex; venation anastomosing; areoles irregular elongate rhomboidal, becoming narrower distally; vein density across mid-pinna c. 12/10 mm.

Description

A small pinnate frond, base missing; rachis at broken base 2 mm wide. Pinnae semi-dorsally attached, basally at c. 100°, in mid-frond at 90° and becoming slightly acute apically; confluent; succeeding pinnae increasing in length from short ovate to elongate-oblong or broad-elliptic; pinnae at mid-frond 22 mm long, variable in width from 11–15 mm, tapering to broad obtuse apices; distally the pinnae conjoin to form an entire obtuse *Gontriglossa*-like apex to the frond. Veins attached straight to rachis, forking then anastomosing with adjacent veins to form irregular elongate rhomboidal areoles from 4–10 mm long and 0.6–1 mm wide, becoming shorter and narrower towards the pinna apex, outer veins running parallel to margin and terminating around the pinna apex; vein density across mid-lamina c. 12/10 mm.

Holotype

AMF134031 and counterpart AMF134032, Australian Museum, Sydney.

Type locality

Reserve Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name derivation

marniana – for Marnie Holmes-Kaner, daughter of the senior author, a keen-eyed helper on collecting trips.

Discussion

The entire apex of AMF134031 (Fig. 22A) is reminiscent of the apices of Triassic *Glossopteris*-like leaves (Holmes 1992) now placed in the genera *Gontriglossa* and *Cetiglossa* by Anderson and Anderson (1989, 2003). *Ctenis màrniana* differs from *C.* sp. *A* (below) by the shorter rounded pinnae and the less dense venation forming irregular and less elongate areoles.

Two species of *Ctenis* have been recorded from the Molteno Formation of South Africa by Anderson and Anderson (1989, p. 343). *Ctenis biloba* differs from the Nymboida specimens by the lobed pinna apices and denser venation; *C.* sp. *A* (of Anderson and Anderson 1989) differs by the contracted acroscopic pinna bases and is possibly bipinnate. Detached pinna fragments occur in the Ipswich Coal Measures of Queensland. *Ctenis* sp. *1* of Jones and DeJersey (1948, figs 27, 28) differs from the Nymboida material by the acute pinna apices; their *C.* sp. *2* (Fig. 29) differs by the irregular, fewer and more elongate anastomoses.

Ctenis sp. *A*

Figures 23B; 24B, C

Description

Part and counterpart of a mid-portion 90 mm long of a medium-sized frond, rachis 2 mm wide. Pinnae well-separated, decurrent, opposite to alternate, attached semi-dorsally at c. 80°, constricted slightly near the base, lanceolate to 50 mm long, adjacent pinnae irregular in width, from 6–12 mm wide, apices broad-obtuse. Some veins forking close to the rachis then irregularly throughout the lamina to anastomose with adjoining veins to form very elongated narrow areoles to 20 mm long, 0.5–1 mm in width, becoming shorter and narrower close to the pinna apex; outer veins running parallel to margin and all veins terminating around pinna apex. Vein density across mid-lamina c. 14–16/10 mm.

Material

AMF134034a and counterpart 134034b, Reserve Quarry.

Discussion

Ctenis sp. *A* differs from *C. marniana* (above) by the more elongate pinnae and narrower elongate areoles. However both forms occur in a grey siltstone from the same horizon, which suggests that they may belong to a single species bearing pinnae with extremely variable form and venation pattern.

Order Bennettitales
Family incertae sedis

Genus *Halleyoctenis* Anderson and Anderson 1989

Type species

Halleyoctenis megapinnata (Anderson and Anderson 1989).

The genus *Halleyoctenis* was erected by Anderson and Anderson (1989) for cycad leaves distinguished by very fine and closely-spaced veins that bifurcate and radiate to the lamina margin. The cuticle preserved on Molteno specimens of *H. megapinnata* has non-aligned probably haplocheilic stomata that indicate an affinity with the Bennettitales. Anderson and Anderson selected as the genotype the leaf originally described and illustrated by Shirley (1897, fig. 7a) from the Ipswich Coal Measures of Queensland as *Pterophyllum multilineatum;*[see also Shirley (1898) and Walkom (1917)]. We have examined this specimen (correct number QGS161) in the QGS collections in Brisbane. The venation, where clearly preserved, is not radiating but straight and parallel and terminates at the pinna apex. The cuticle is not preserved. We also examined the specimens UQF31692, 72854 and 9922 that were described by Webb (1980) in his unpublished thesis and illustrated by Anderson and Anderson (1989, p. 328, t. figs 5-8) as *Halleyoctenis multilineata.* Two of these specimens show fine veins (38-40/10 mm) running parallel to the apex and compare well with Shirley's original specimen. The drawing of UQF31692 in Anderson and Anderson (1989, p. 328, t. fig. 8) is not correct and should be disregarded. From this evidence we conclude that Shirley's type specimen is not a *Halleyoctenis* and a new type is required for that genus. We therefore nominate a new genotype *Halleyoctenis megapinnata* specimen BP/2/1817 as illustrated by Anderson and Anderson (1989, p. 329, t. fig. 1 and Pl. 189, figs 1, 9, 10).

The material from Chile described in Herbst and Troncoso (2000, pp 285–6; fig. 4G) as *Pseudoctenis multilineata* would be best placed in *Halleyoctenis megapinnata*. We agree with Anderson and Anderson (1974, Table 3) and Herbst and Troncoso (2000) that *Pterophyllum multilineatum* – based only on Shirley's type specimen – is better placed in the genus *Pseudoctenis*.

***Halleyoctenis brachypinnata* Anderson and Anderson 1989**

Figures 25A–C

References

1989 Halleyoctenis brachypinnata, Anderson and Anderson p. 328, Figs 1–4, Pls 191–194.
2003 Halleyoctenis brachypinnata, Anderson and Anderson pp 344, 345, figs 1–2.

Description

Part and counterpart of a 95 mm long portion of a frond with the base and apex missing. Rachis 3 mm wide, striated. Pinnae attachment semi-dorsal, at c. 90° to rachis. Pinnae well-separated, opposite to sub-opposite, short to elongated-oblong, increasing in size distally along the rachis, from 12–25 mm long and from 6–8 mm wide, base slightly expanded, margin entire and apex obtuse. Veins emerging straight from rachis, most forking close to base of lamina and a few dividing again throughout the lamina, radiating slightly and terminating around the lamina margin and apex; vein density in mid-lamina c. 44/10 mm.

Material

AMF134035, 134036, Reserve Quarry.

Discussion

The material available is the part and counterpart of an incomplete specimen showing the lower and mid-portion of the frond (Fig. 25A, B). It is placed tentatively with *H. brachypinnata* from the Molteno flora, but differs slightly by the more widely-spaced pinnae that do not expand distally. It is distinct from *H. megapinnata* by the smaller size and lower length/ breadth ratio of the pinnae and from *H. symmetrica* by the oblong pinna shape and uncontracted pinna bases. Anderson and Anderson (2003) suggest that *H. symmetrica* may be generically distinct.

CONCLUSIONS

While cycadophyte fronds are infrequent in the Nymboida flora they are diverse and are placed in fifteen taxa in the cycadalean genera *Pseudoctenis*, *Moltenia* and *Ctenis* and one in the bennettitalean genus *Halleyoctenis*. Some forms compare well with material from the Molteno Formation of South Africa (*Pseudoctenis fissa, P. sanipassiensis, Halleyoctenis brachypinnata*), La Ternera Formation of Chile and the Barreal Formation of Argentina (*Pseudoctenis azcaratei*) and the Brady Formation of Tasmania (*Pseudoctenis* sp. cf *P. strahanii*). Fronds considered distinct are described as the eight new species *Pseudoctenis nymboidensis*, *P. rigbyi*, *P. prolongata*, *P. cursanervia*, *P. grandis*, *P. nettiana*, *Moltenia sparsispinosa* and *Ctenis marniana*. Insufficiently complete but clearly distinct material is described as *Pseudoctenis* sp. *A* and *P.* sp. *B* and *Ctenis* sp. *A*. *Pterophyllum azcaratei* is transferred to *Pseudoctenis azcaratei* and *Halleyoctenis megapinnata* is nominated as a new genotype for *Halleyoctenis*. It is believed that the pinnae on all fronds are semi-dorsally attached rather than laterally attached as in some earlier descriptions.

ACKNOWLEDGEMENTS

W.B.K.H. was greatly assisted by his family over the many years of collecting at the Nymboida quarries. A grant from the Betty Mayne Research Fund has contributed to the progress of this project.

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Figure. 1. A, B. *Pseudoctenis fissa* Du Toit. A. AMF133968; B. AMF133963, Coal Mine Quarry. Scale bar =1 cm.

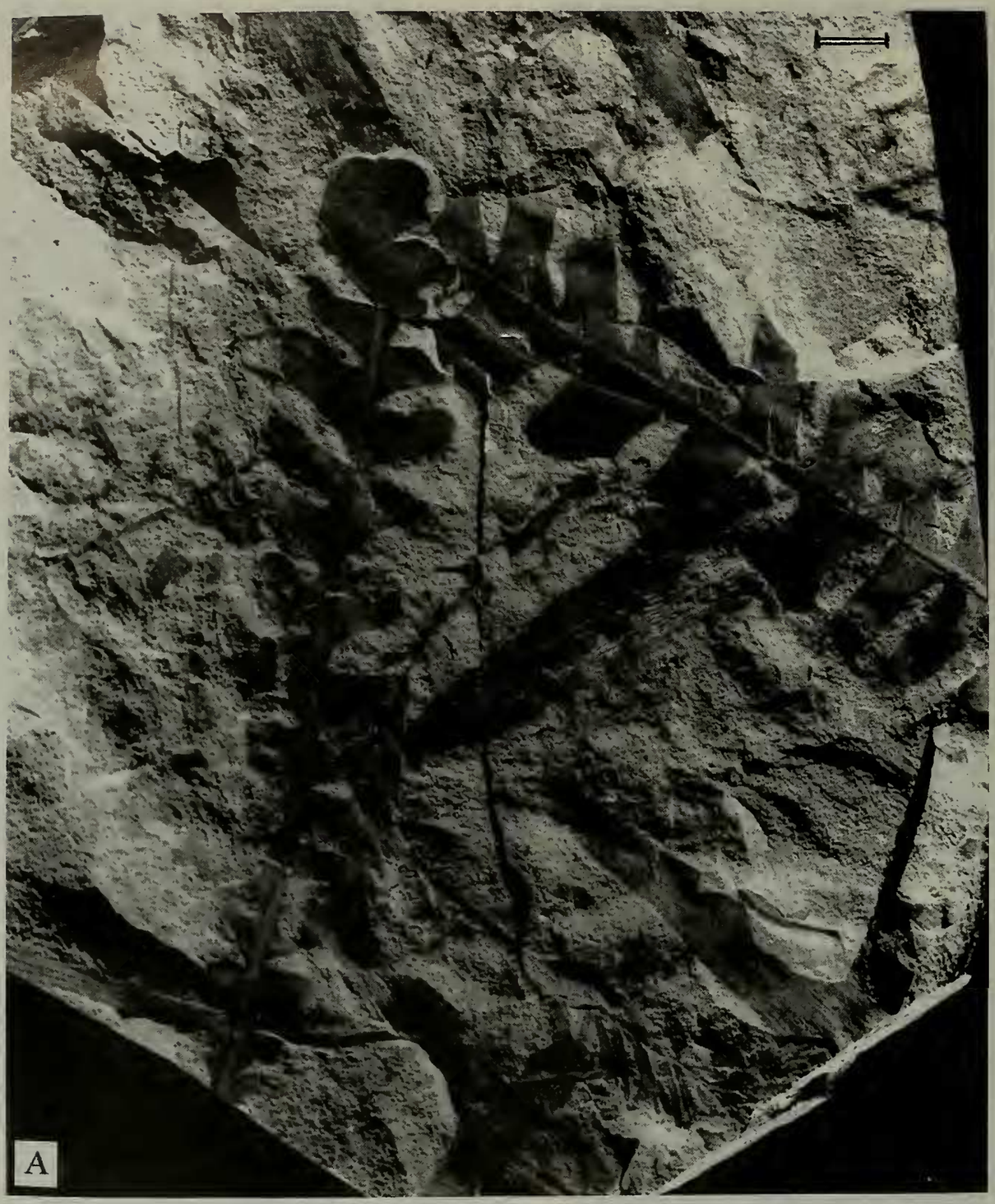

Figure 2. A. *Pseudoctenis fissa* Du Toit. AMF133962, Coal Mine Quarry. Scale bar = 1 cm.

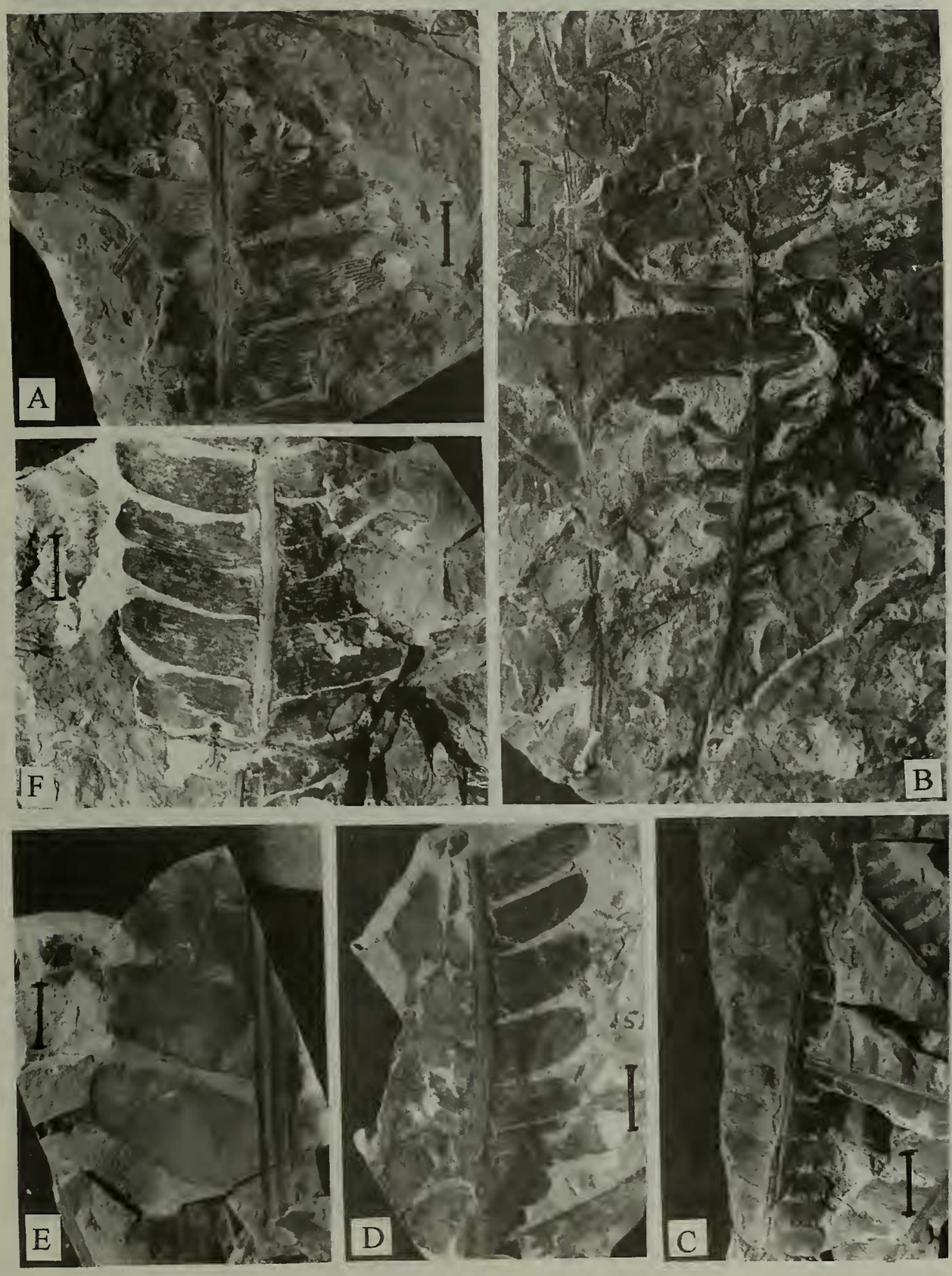

Figure 3. A–F. *Pseudoctenis fissa* Du Toit. A. AMF (133966), Reserve Quarry; B. AMF133960, Coal Mine Quarry; C. AMF133965, Coal Mine Quarry; D. AMF133961, Coal Mine Quarry; E. AMF133967, Reserve Quarry; F. AMF133964, Coal Mine Quarry. Scale bars = 1 cm.

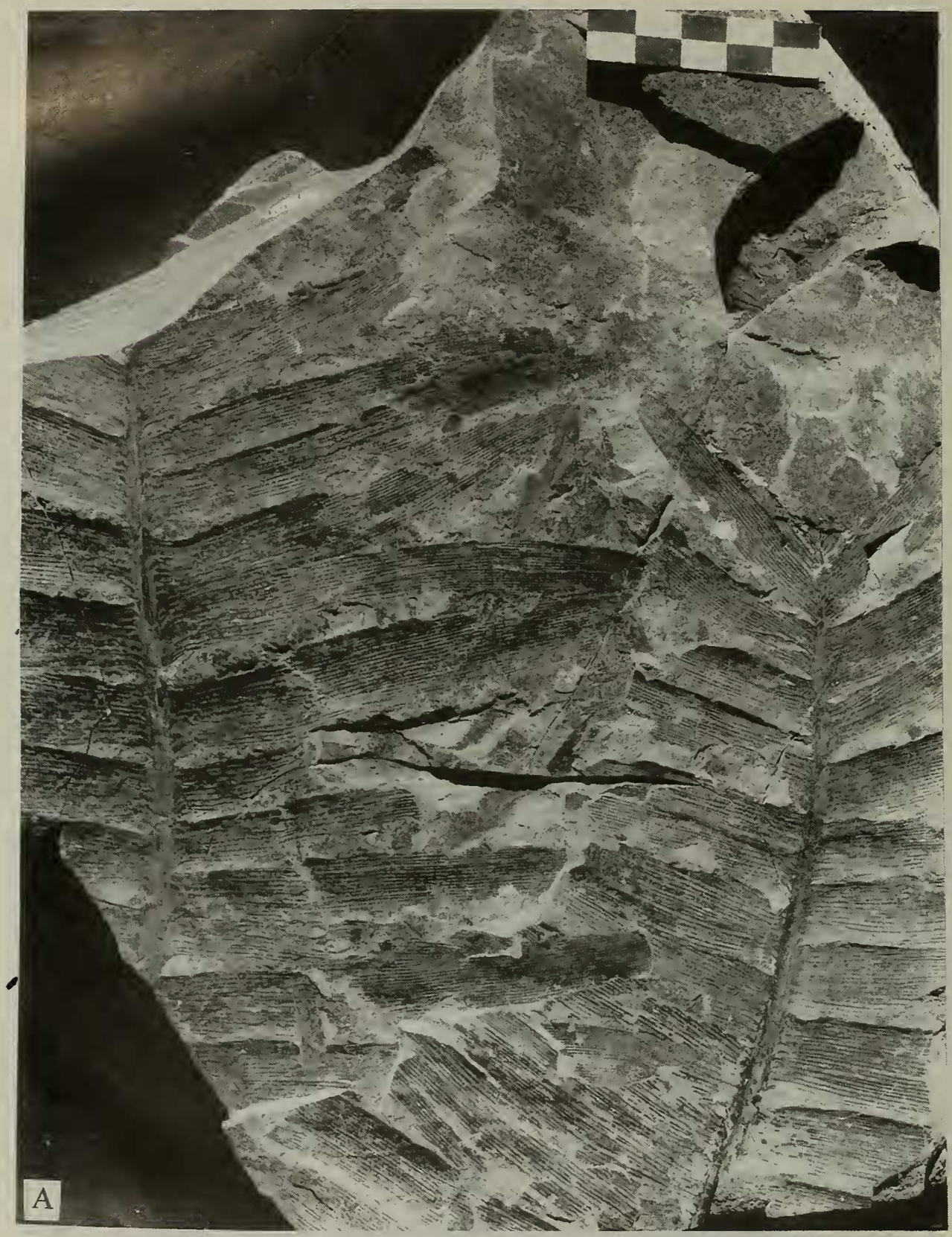

Figure 4. A. *Pseudoctenis nymboidensis* Holmes and Anderson sp. nov. Holotype AMF133969, Coal Mine Quarry. Scale bar = 5 cm.

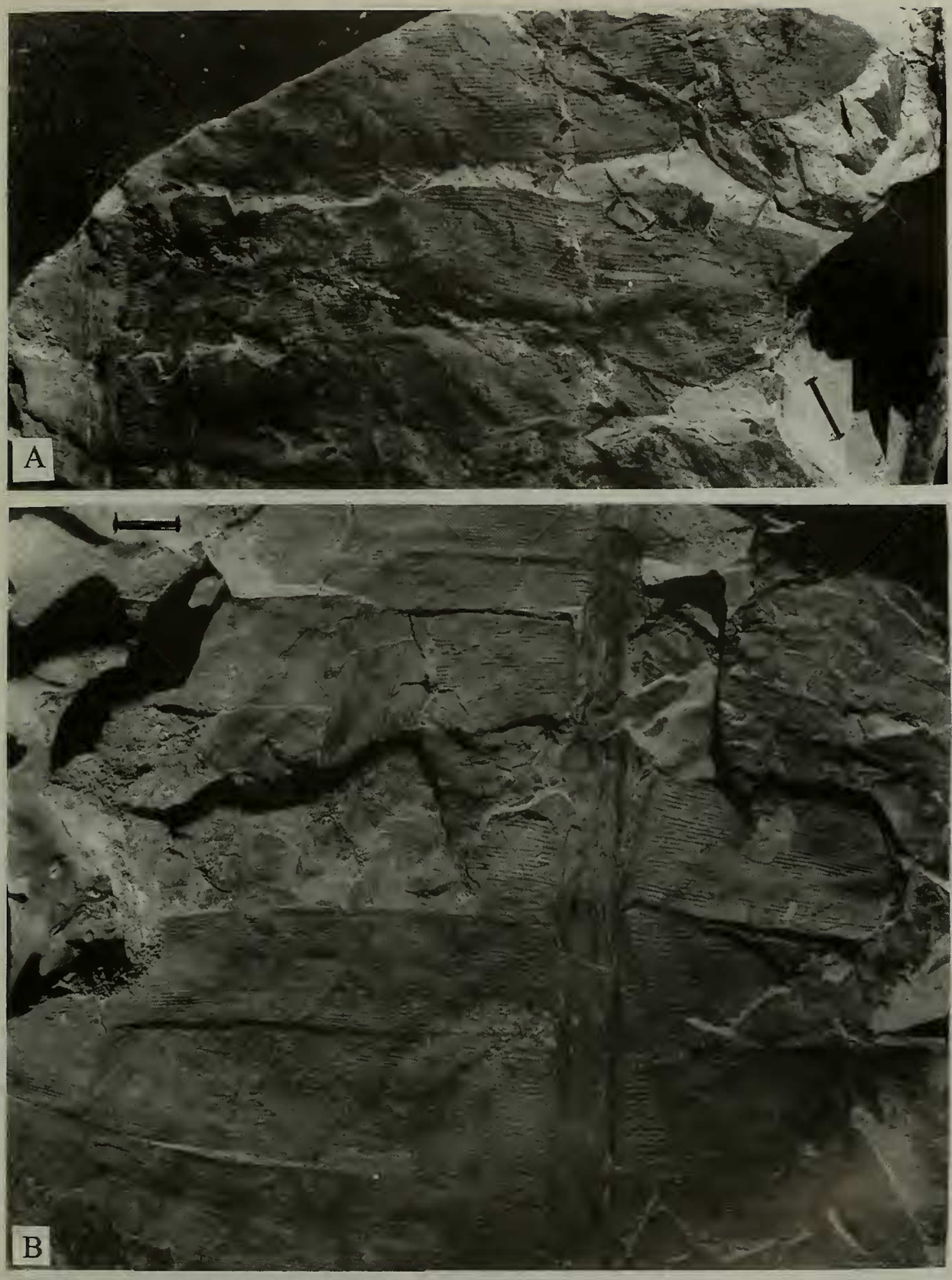

Figure 5. A, B. *Pseudoctenis nymboidensis* Holmes and Anderson sp. nov. A. AMF133972, Coal Mine Quarry; B. AMF133981, Reserve Quarry. Scale bars = 1 cm.

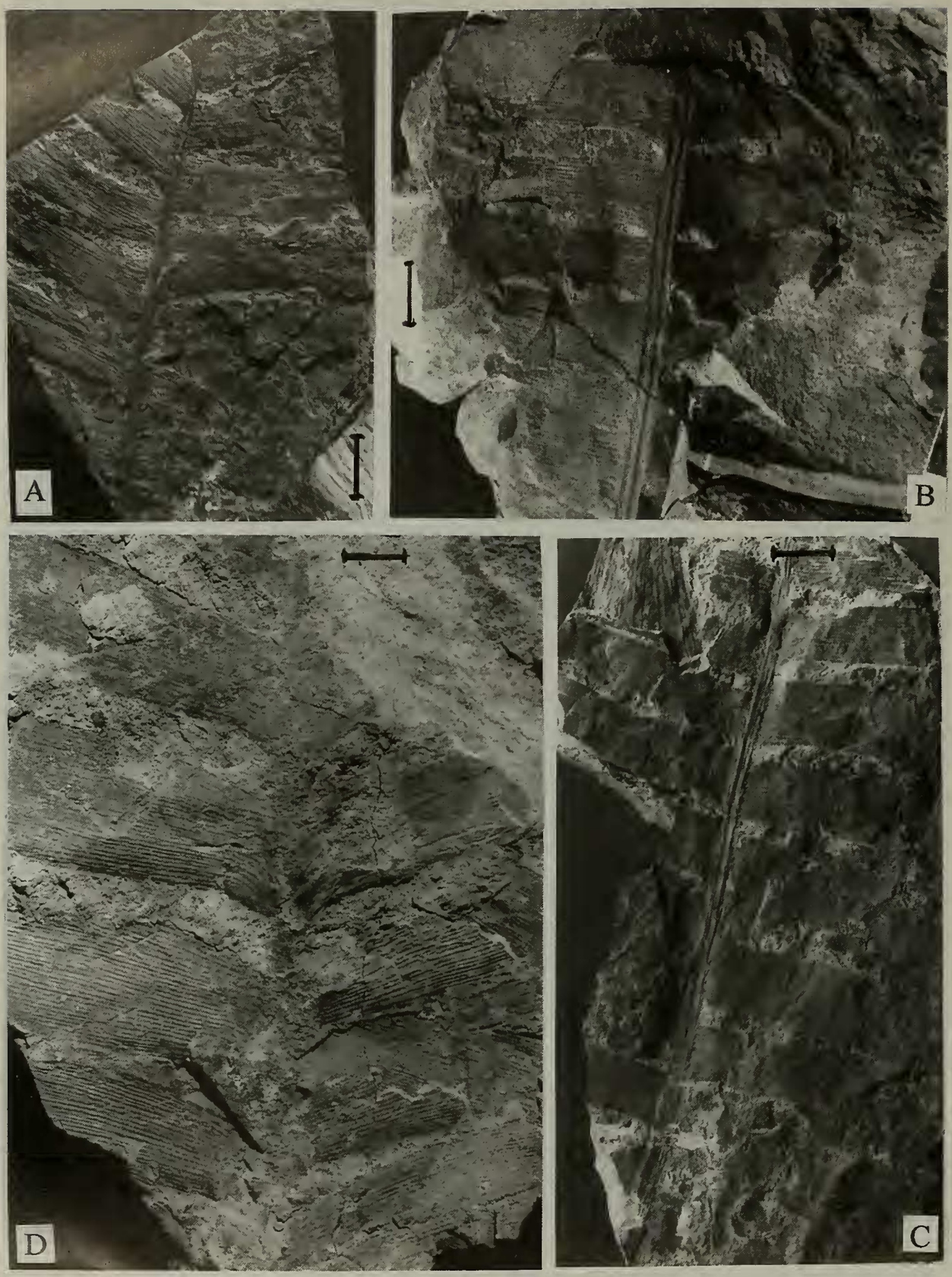

Figure 6. A–E. *Pseudoctenis nymboidensis* Holmes and Anderson sp. nov. A. AMF133976, Coal Mine Quarry; B. AMF126860, Coal Mine Quarry; C. AMF133977, Coal Mine Quarry; D. AMF133980, Reserve Quarry. Scale bars = 1 cm.

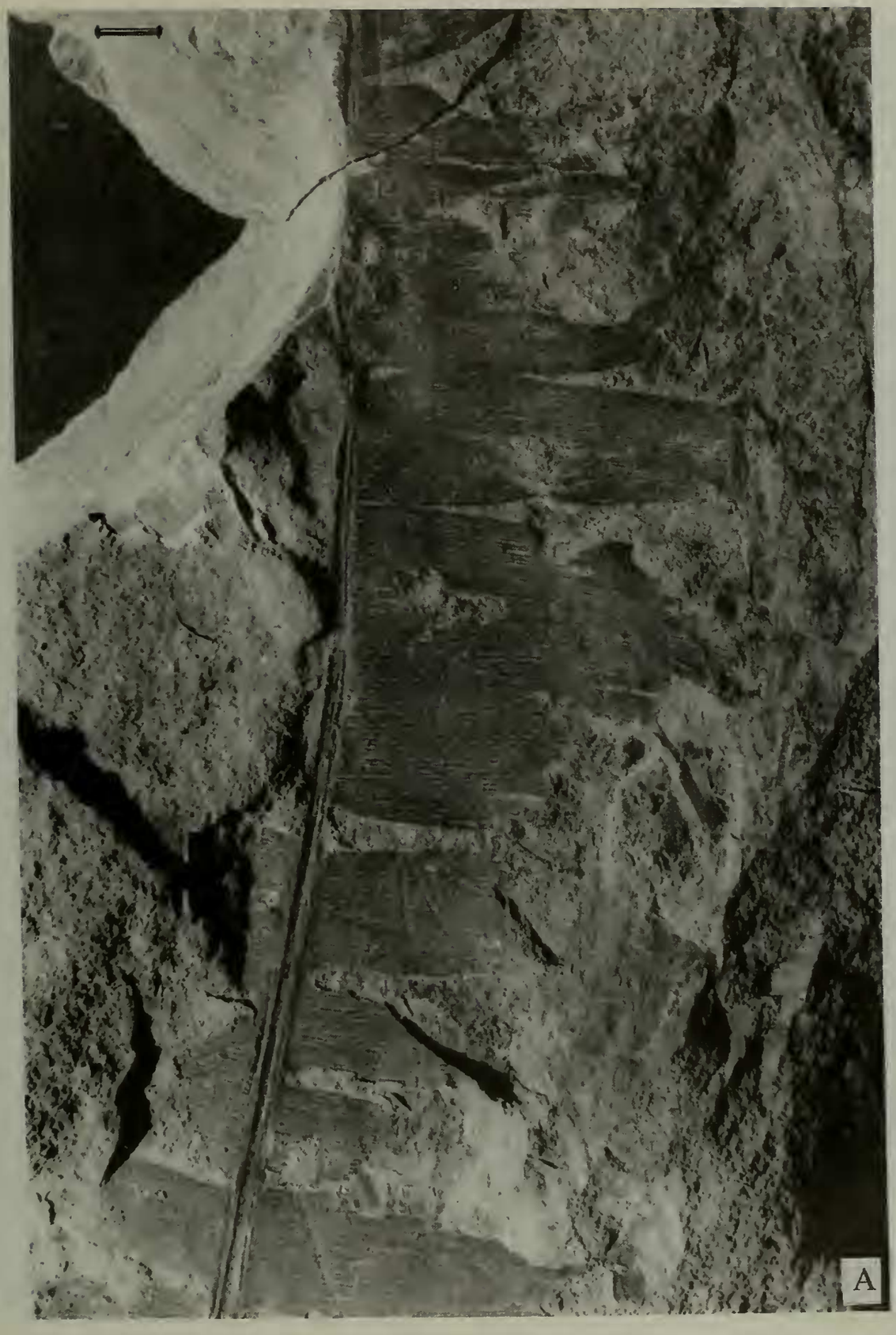

Figure 7. A. *Pseudoctenis nymboidensis* Holmes and Anderson sp. nov. AMF133973, Reserve Quarry. Scale bar = 1 cm.

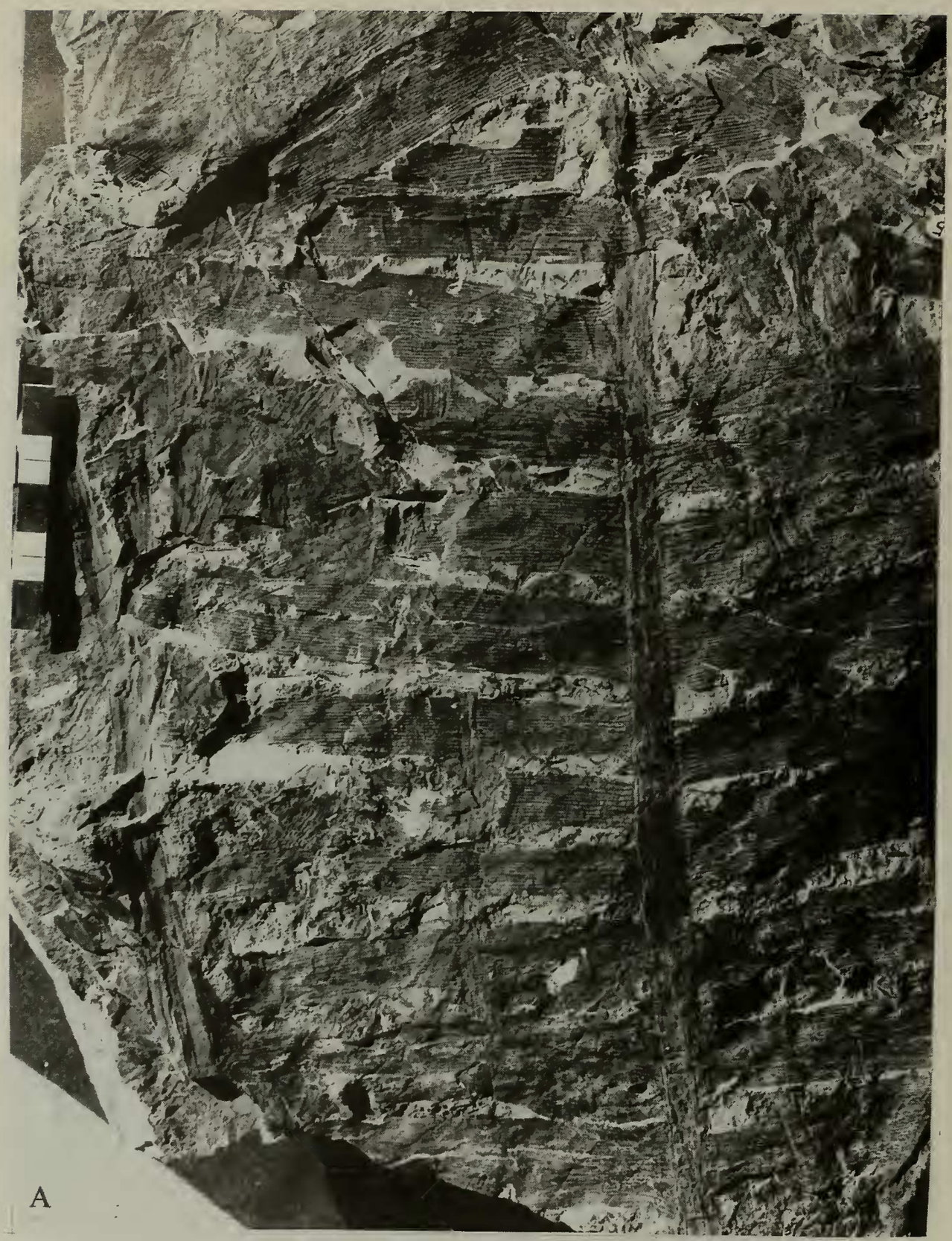

Figure 8. A. *Pseudoctenis nymboidensis* Holmes and Anderson sp. nov. AMF133970, Coal Mine Quarry. Scale bar = 5 cm.

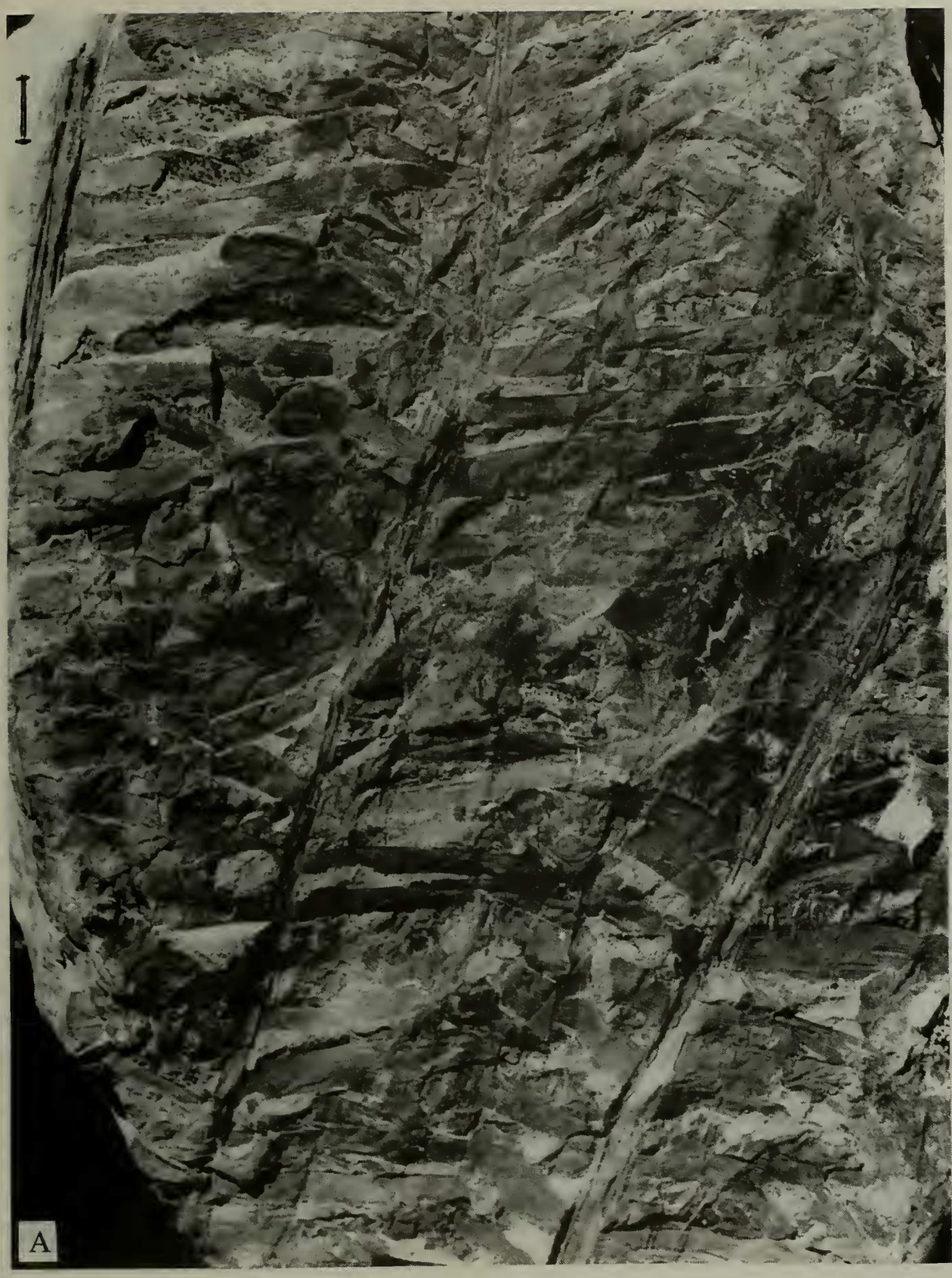

Figure 9. A. *Pseudoctenis rigbyi* Holmes and Anderson sp. nov. Holotype. AMF133982, Coal Mine Quarry. Scale bar = 1 cm.

Figure 10. A. *Pseudoctenis rigbyi* Holmes and Anderson sp. nov. AMF133983, Coal Mine Quarry. Scale bar = 1 cm.

Figure 11. A. *Pseudoctenis sanipassiensis* Anderson and Anderson. AMF133987, Coal Mine Quarry. Scale bar = 5 cm.

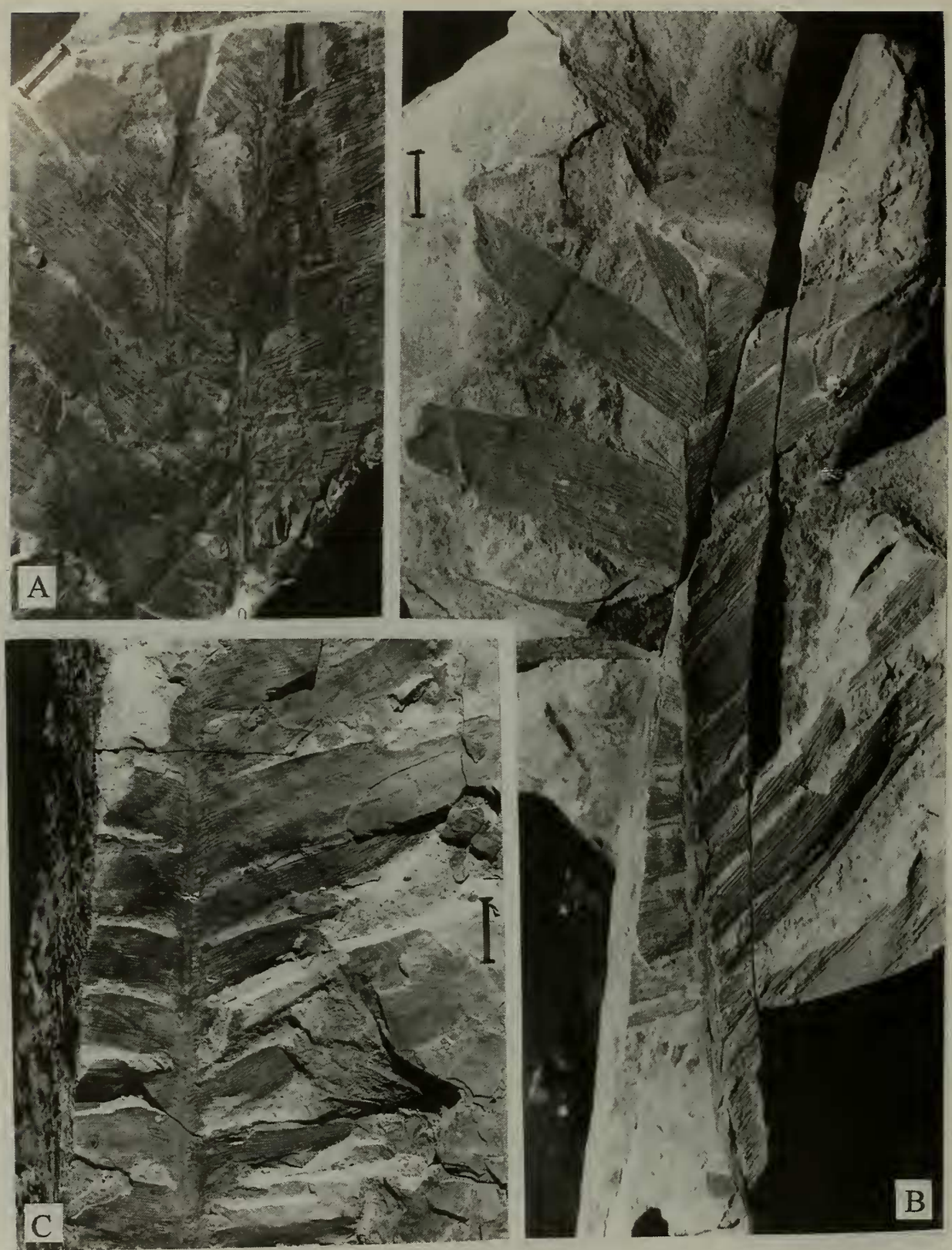

Figure 12. A – C. *Pseudoctenis sanipassiensis* Anderson and Anderson. A. AMF133989; B. AMF133990; C. AMF133994. Coal Mine Quarry. Scale bars = 1 cm.

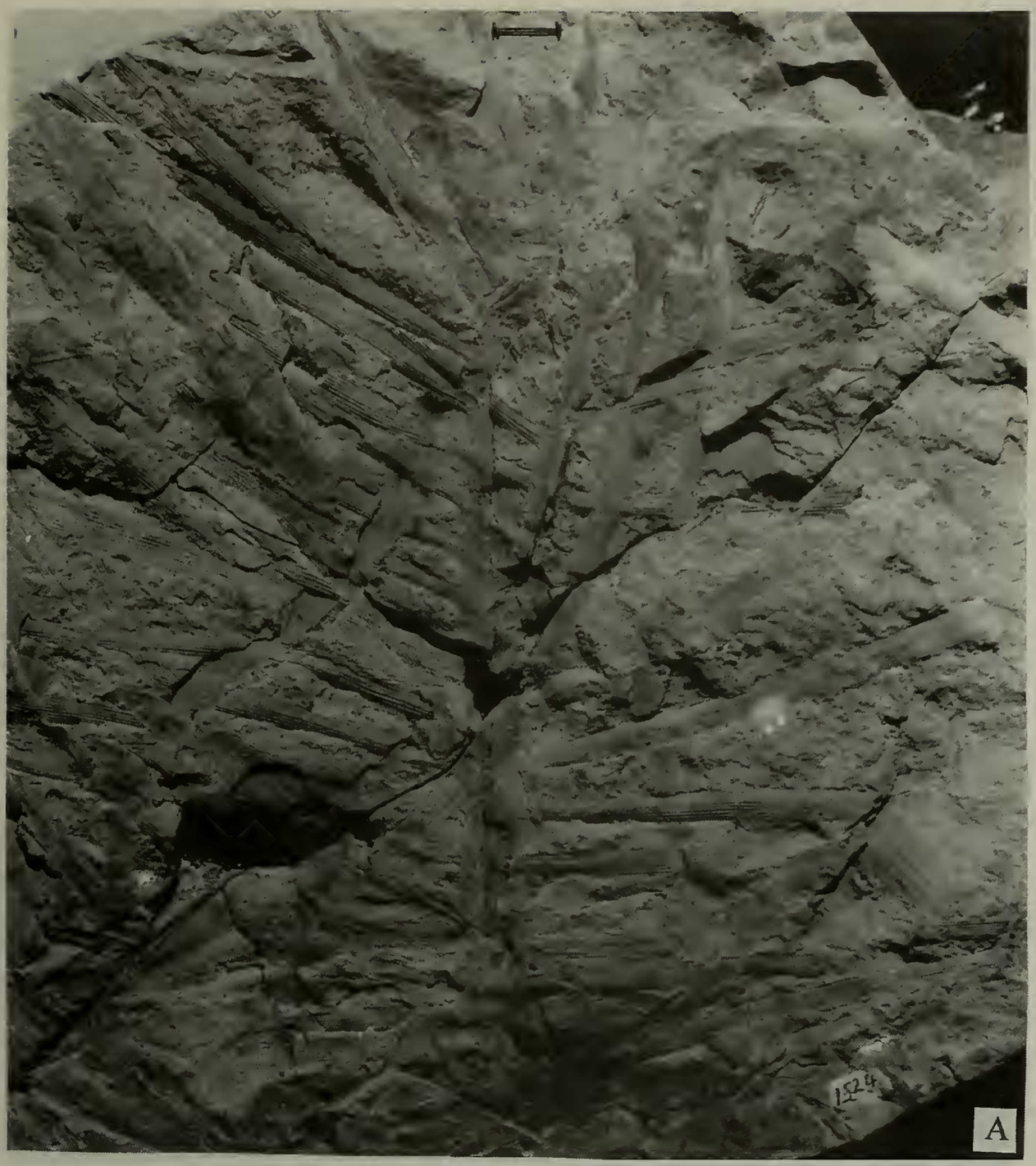

Figure 13. A. *Pseudoctenis prolongata* Holmes and Anderson sp. nov. Holotype. AMF133996, Coal Mine Quarry. Scale bar = 1 cm.

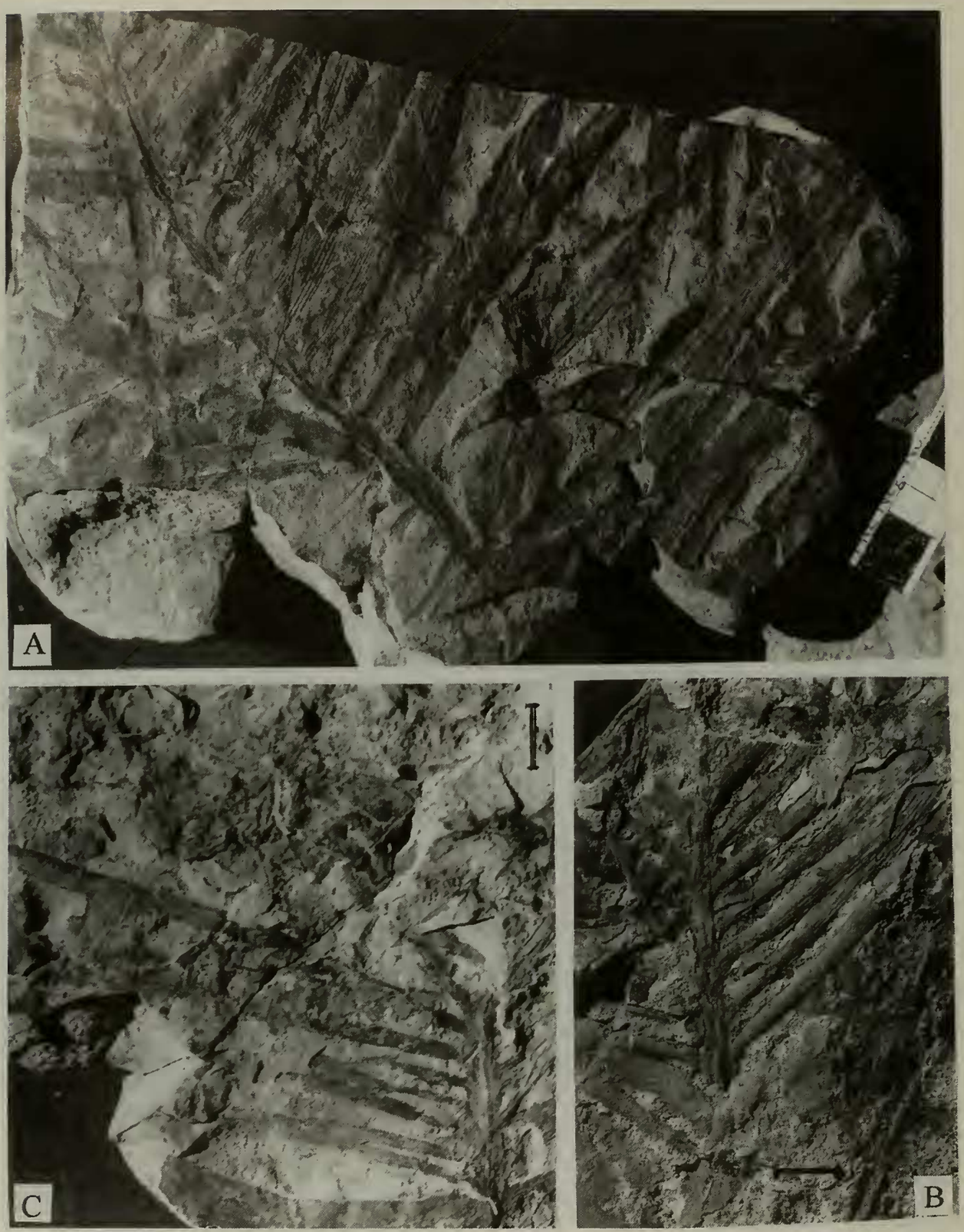

Figure 14. A – C. *Pseudoctenis prolongata* Holmes and Anderson sp. nov. A. AMF133999, Coal Mine Quarry; B. AMF133998, Coal Mine Quarry; C. AMF133400, Reserve Quarry. Scale bars = 1 cm.

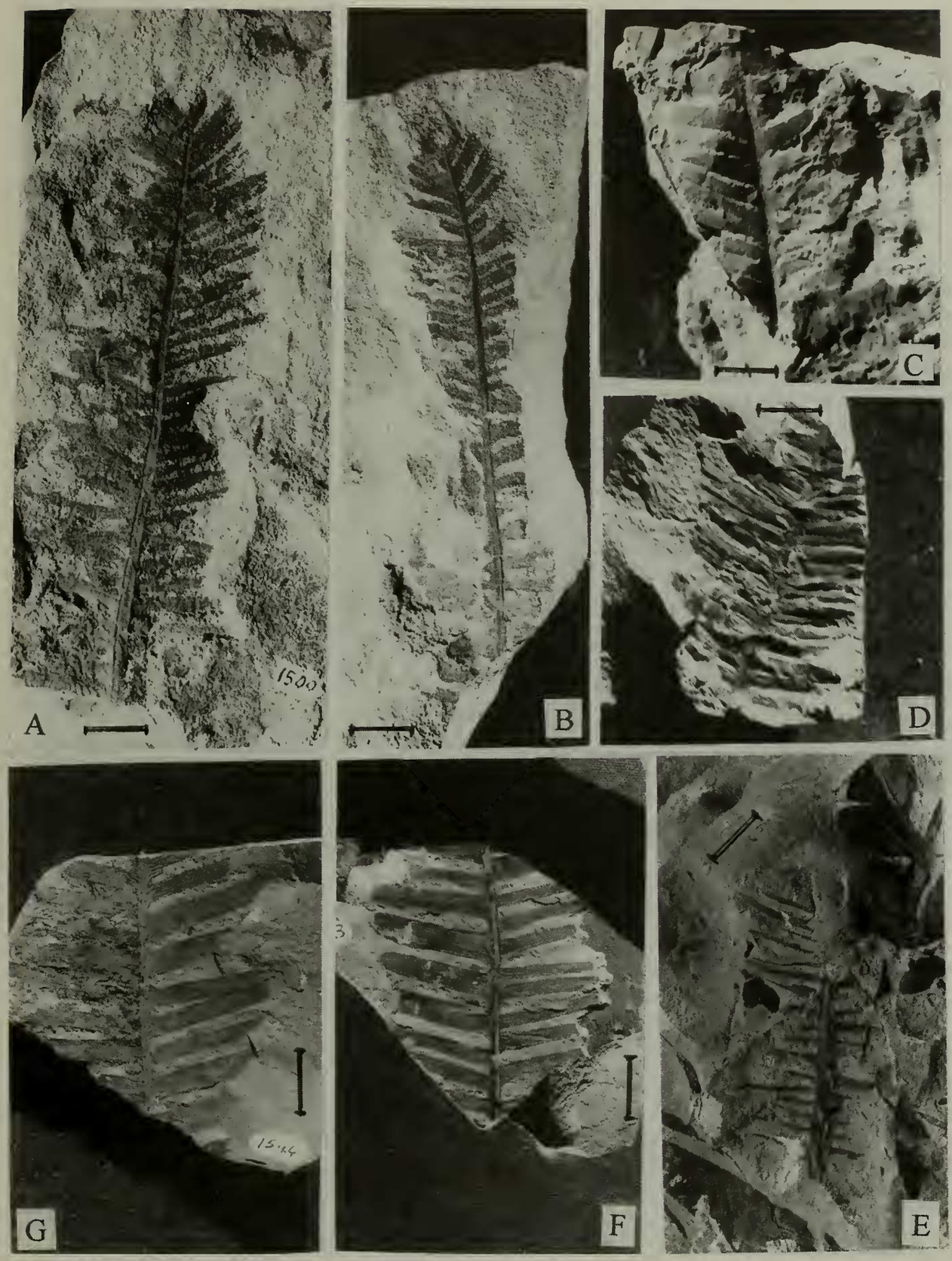

Figure 15. A–G. *Pseudoctenis nettiana* Holmes and Anderson sp. nov. A. Holotype. AMF134003, Coal Mine Quarry; B. AMF134004, Coal Mine Quarry; C. AMF134005, Coal Mine Quarry; D. AMF134008, Coal Mine Quarry; E. AMF134011, Reserve Quarry; F. AMF134002, Coal Mine Quarry; G. AMF134007, Coal Mine Quarry. Scale bars = 1 cm.

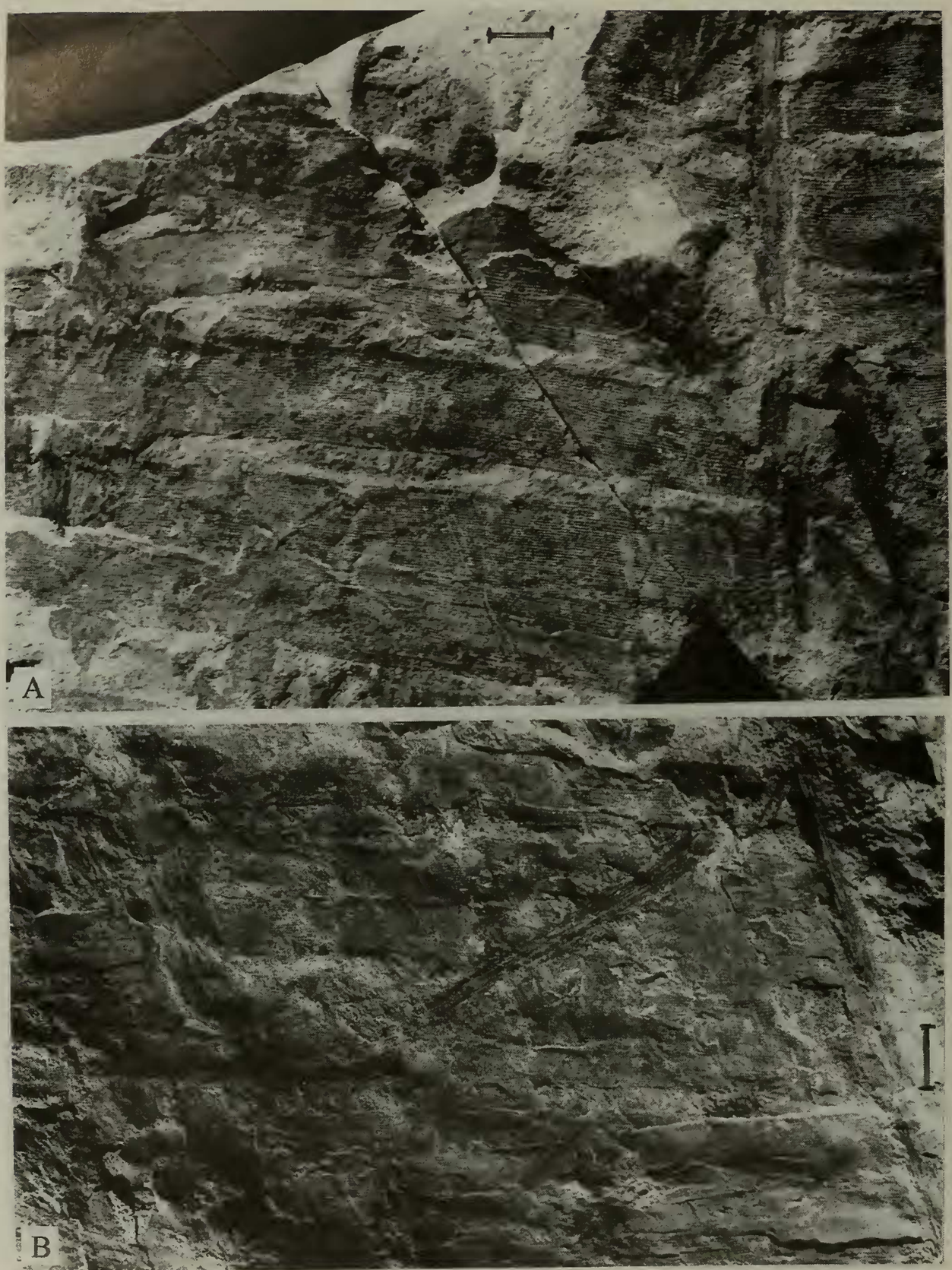

Figure 16. A, B. *Pseudoctenis grandis* Holmes and Anderson sp. nov. A. Holotype. AMF134012; B. AMF134013. Coal Mine Quarry. Scale bars = 1 cm.

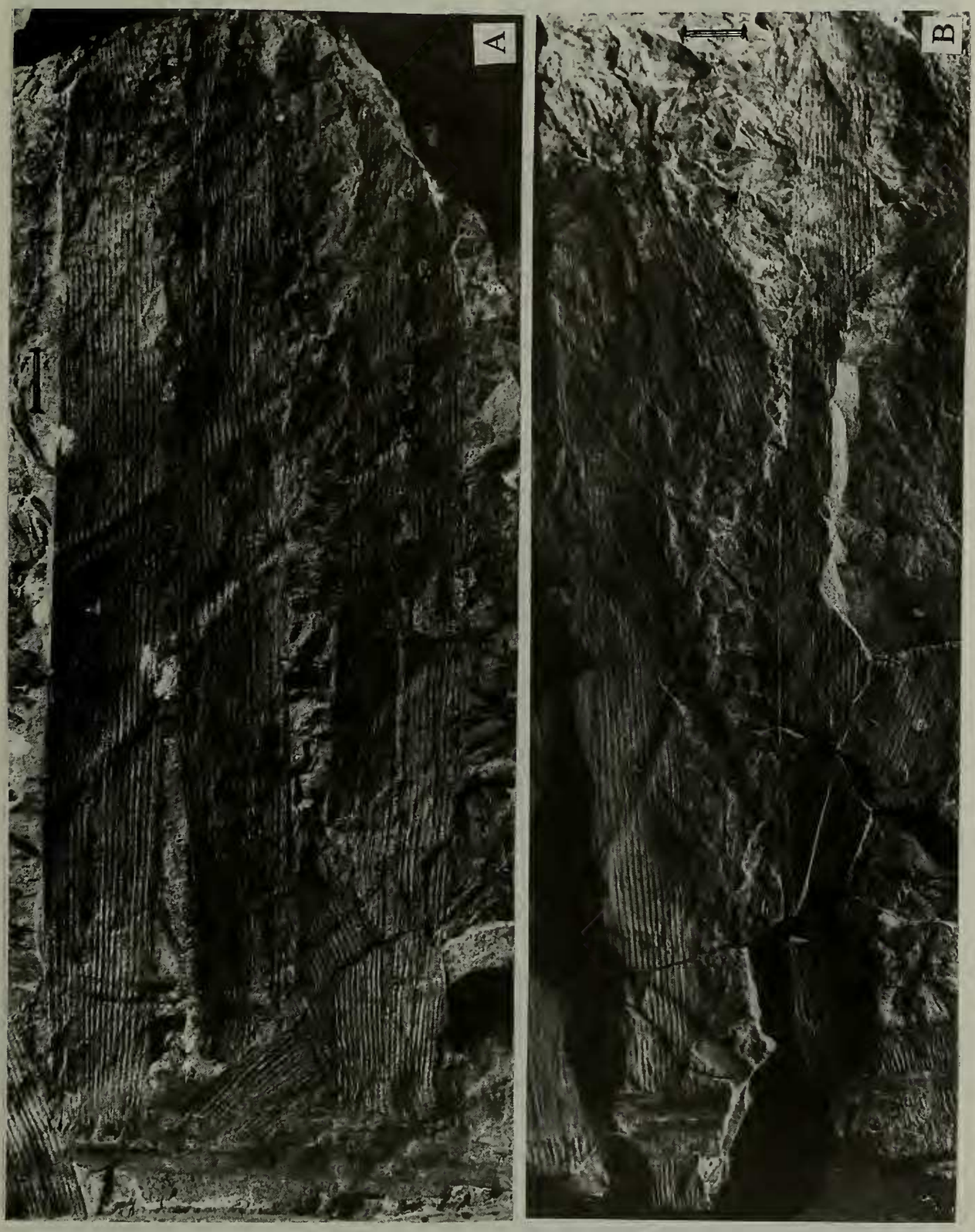

Figure 17. A, B. *Pseudoctenis cursinervia* Holmes and Anderson sp. nov. A. Holotype AMF134016; B. AMF134017, Coal Mine Quarry. Scale bars = 1 cm.

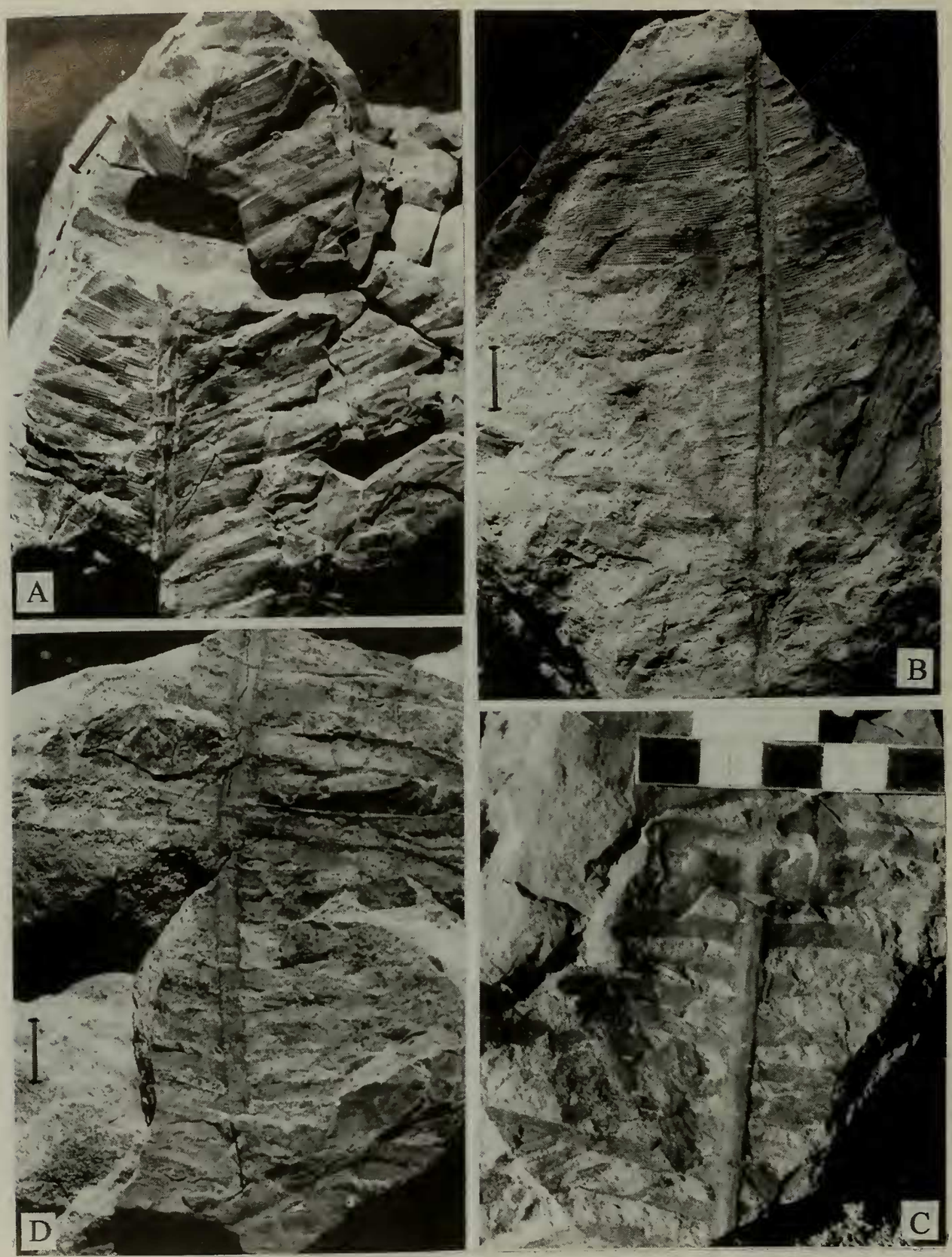

Figure 18 A–D. *Pseudoctenis azcaratei* (Herbst and Troncoso) Holmes and Anderson comb. nov. A. AMF134020; B. AMF134018; C. AMF134022; D. AMF134019. Coal Mine Quarry. Scale bars = 1 cm.

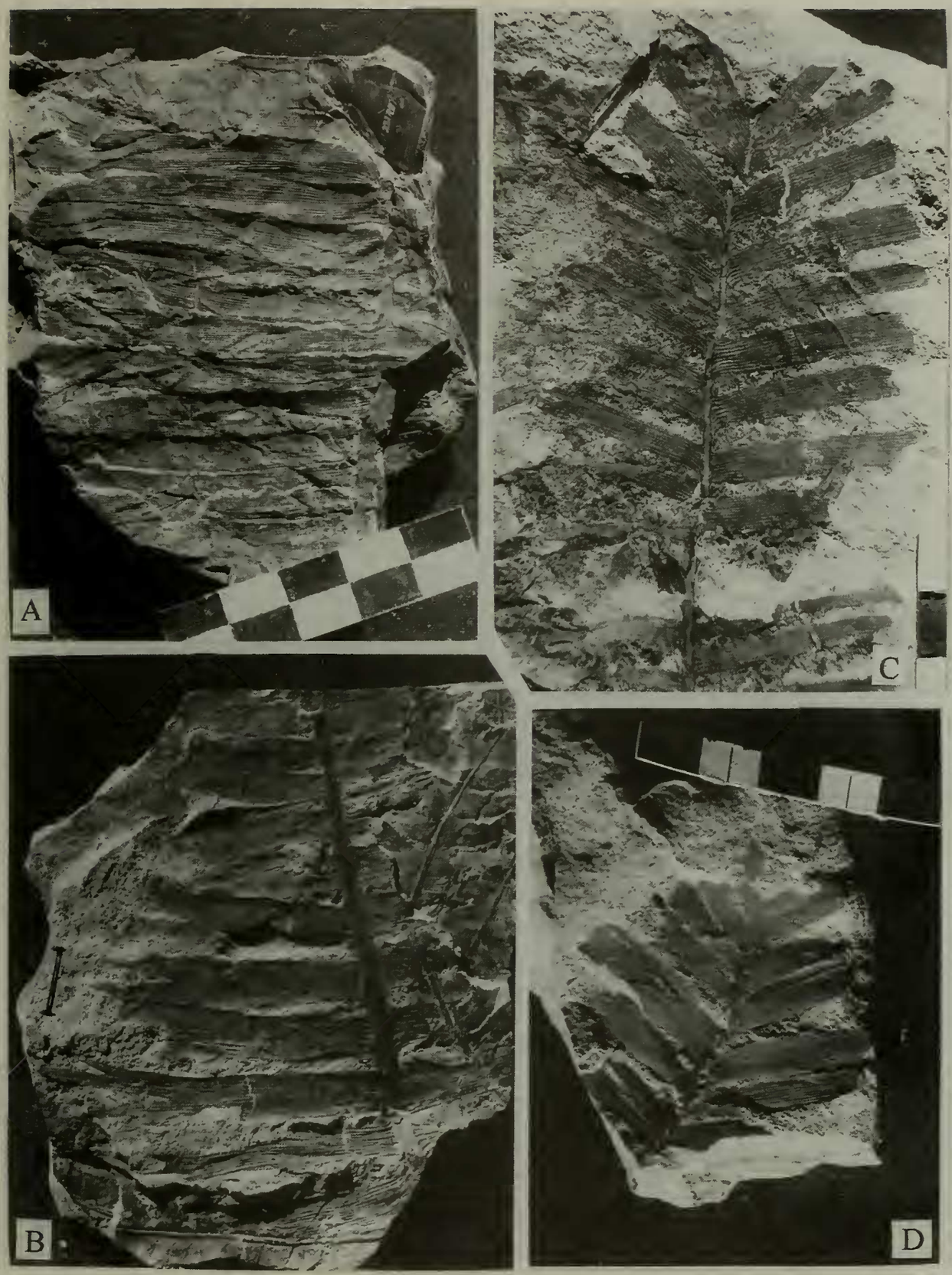

Figure 19. A. *Pseudoctenis azcaratei* (Herbst and Troncoso) Holmes and Anderson comb. nov. AMF134021, scale bar = 5 cm.; B. *Pseudoctenis* sp. cf. *Pseudoctenis strahanii* (Johnston) Anderson and Anderson, AMF134023, scale bar = 1 cm.; C, D. *Pseudoctenis* sp. A; C. AMF134024, scale bar = 1 cm.; D. AMF134025, scale bar = 5 cm. All Coal Mine Quarry.

Figure 20. A. *Moltenia sparsispinosa* Holmes and Anderson sp. nov. A. Holotype. AMF134028, Coal Mine Quarry. Scale bar = 5 cm.

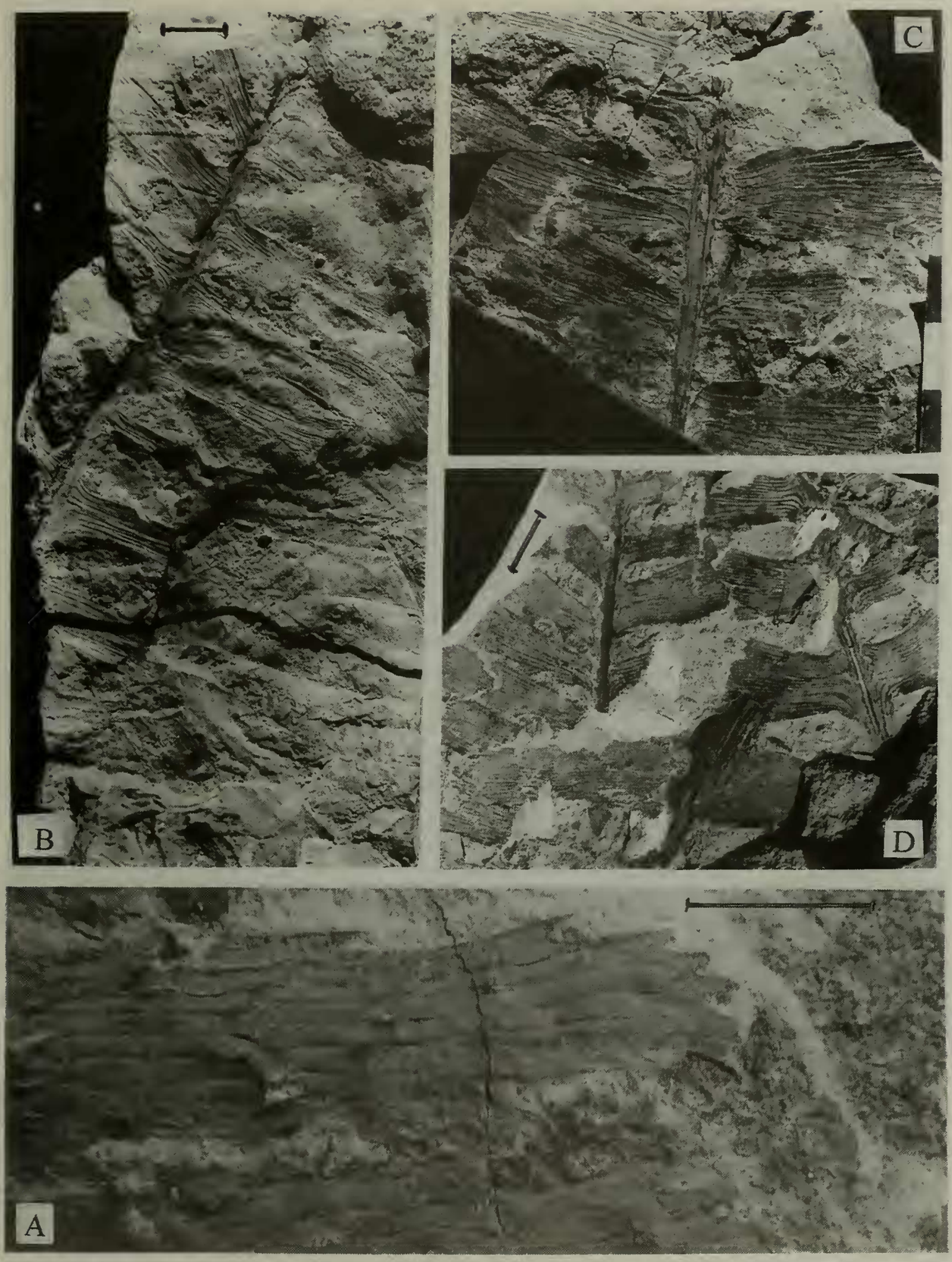

Figure 21. A–D. *Moltenia sparsispinosa* Holmes and Anderson sp. nov. A. AMF134033, paratype, Reserve Quarry; B. AMF134030, Reserve Quarry; C. AMF134029, Coal Mine Quarry; D. AMF134027, Coal Mine Quarry. Scale bars = 1 cm.

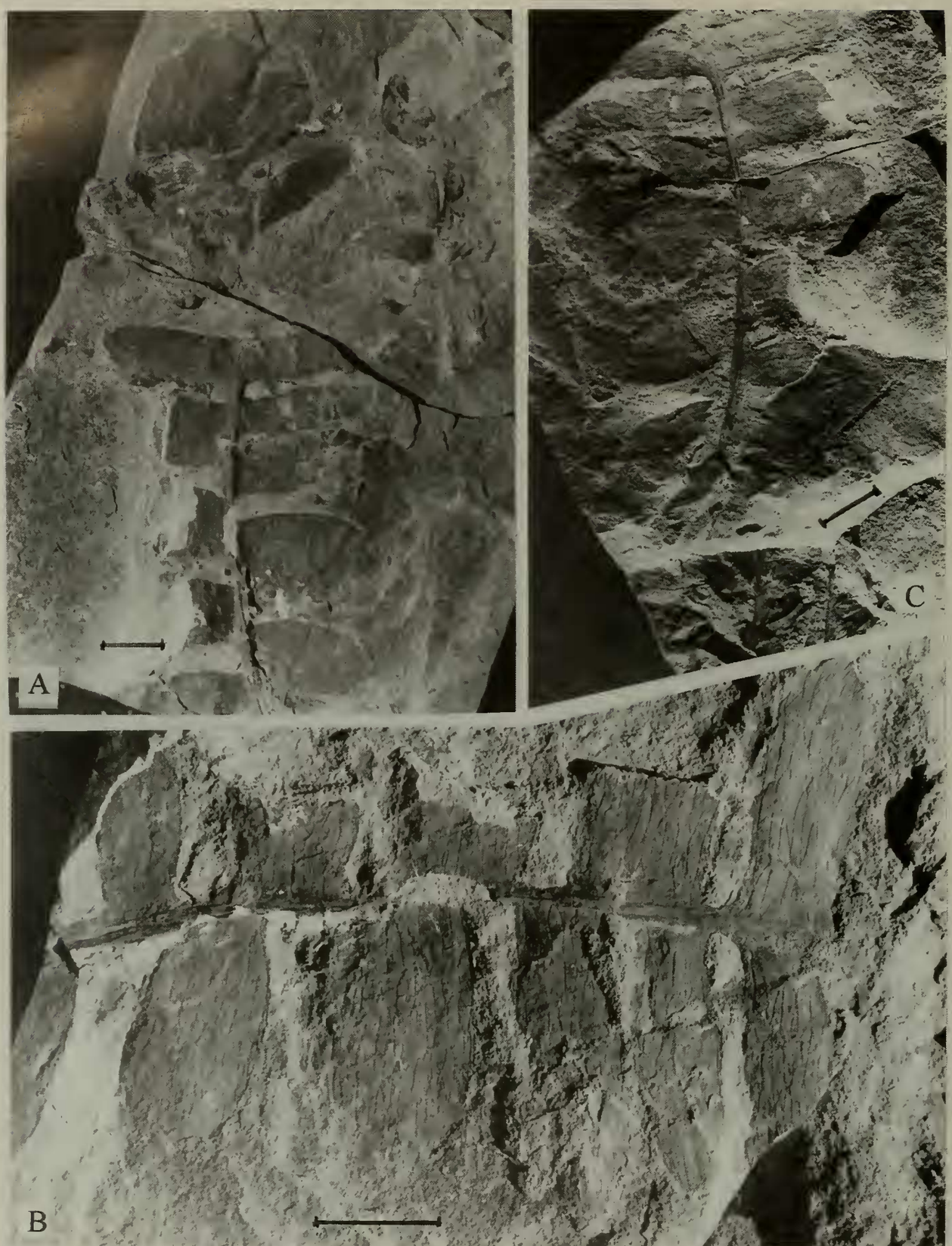

Figure 22. A–C. *Ctenis marniana* Holmes and Anderson sp. nov. A, B. Holotype AMF134031; C. AMF134032, counterpart of Holotype, Reserve Quarry. Scale bars = 1 cm.

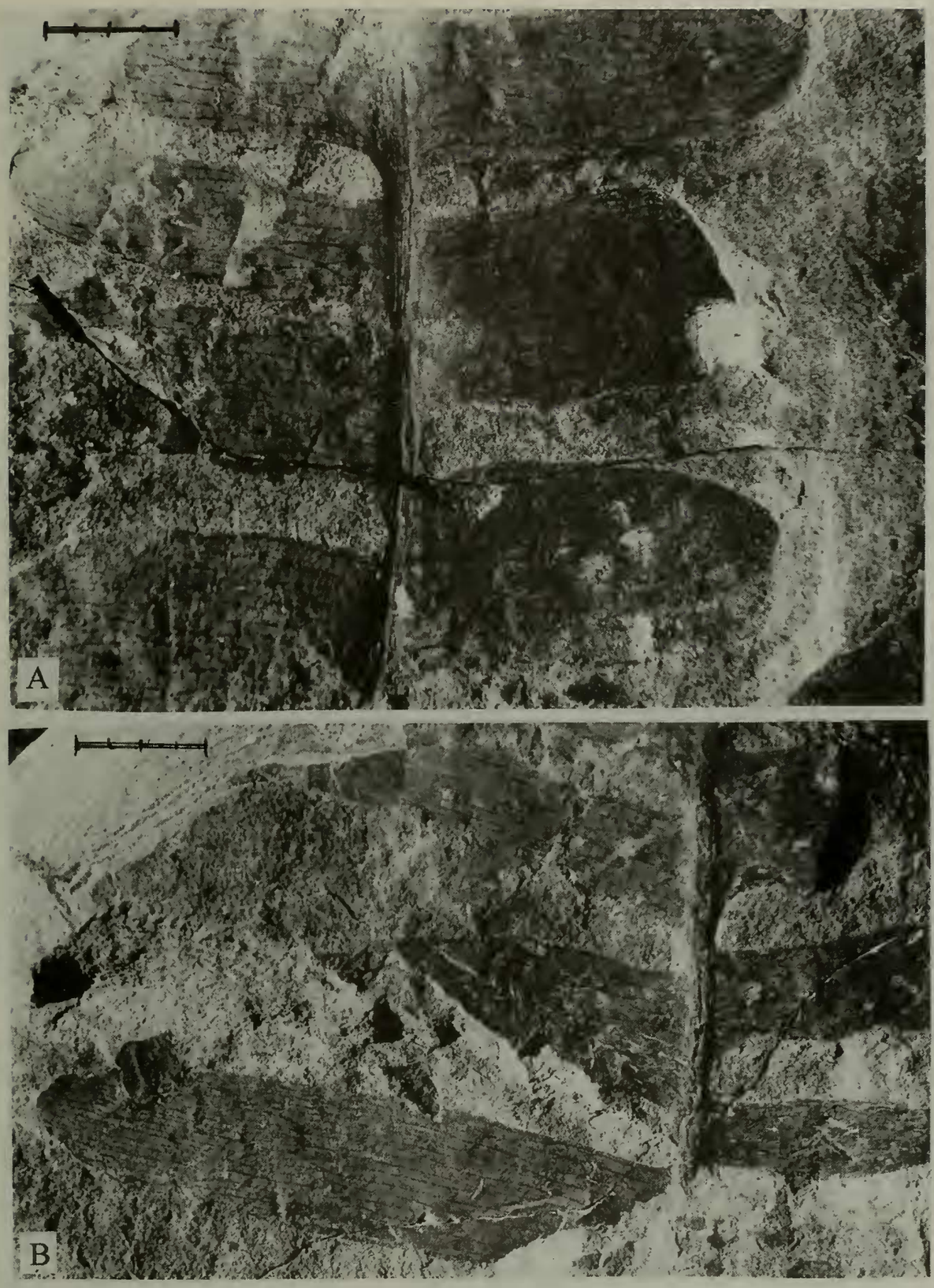

Figure 23. A. *Ctenis marniana* Holmes and Anderson sp. nov. AMF134032; B. *Ctenis* sp A. AMF134034. Reserve Quarry. Scale bars = 1 cm.

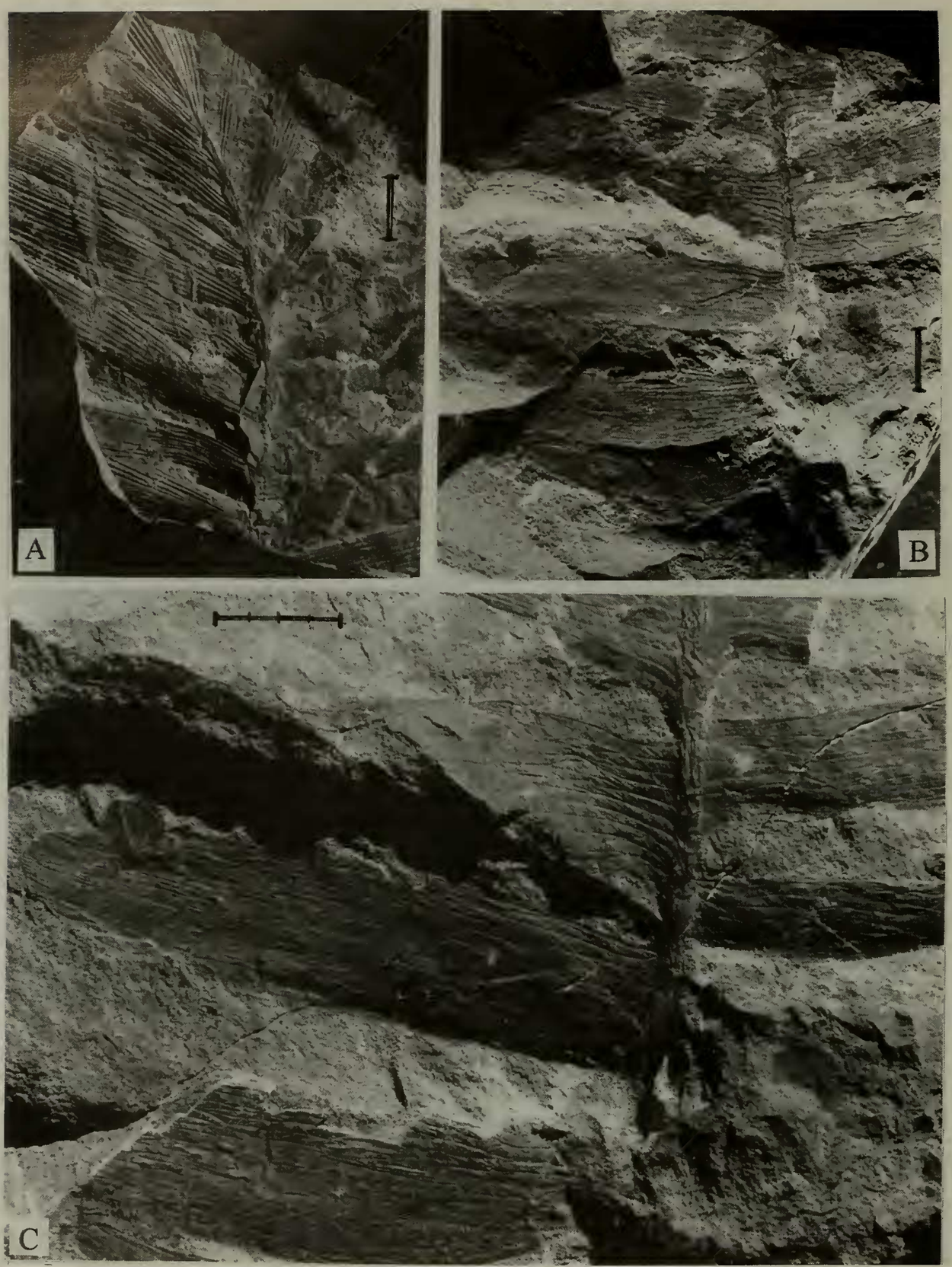

Figure 24. A. *Pseudoctenis* sp. B. AMF134026, Coal Mine Quarry; B, C. Ctenis sp. A. AMF134034, Reserve Quarry. Scale bars = 1 cm.

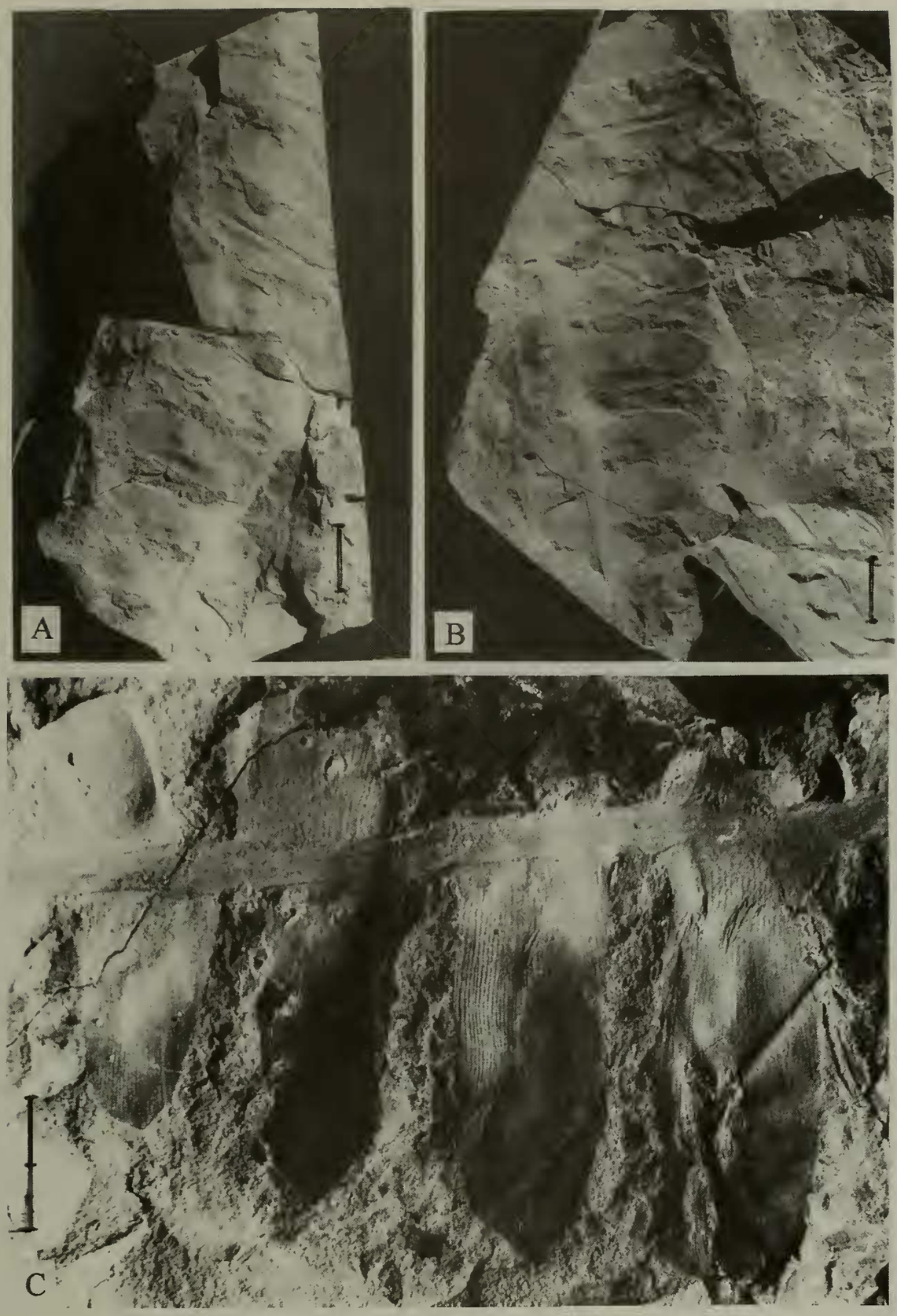

Figure 25. A–C. *Halleyoctenis brachypinnata* Anderson and Anderson. A. AMF134036; B, C. AMF134035. Reserve Quarry. Scale bars = 1 cm.